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The Ecology of Rabies in Northeastern Tennessee

Howard Fleming Hall III
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a dissertation written by Howard Fleming Hall III entitled "The Ecology of Rabies in Northeastern Tennessee." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Michael R. Pelton, Major Professor

We have read this dissertation and recommend its acceptance:

Ralph W. Dimmick, James, T. Tanner, Hyram Kitchen

Accepted for the Council:
Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

THE ECOLOGY OF RABIES IN NORTHEASTERN TENNESSEE

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Howard Fleming Hall III

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ABSTRACT

The study sought to determine the ecological factors which influenced the time and place at which rabid animals occurred in northeastern Tennessee. The study region consisted of 30 counties in North Carolina, Tennessee, and Virginia. Within this region three Tennessee counties, the study area, were selected for detailed field study.

The objectives of the study were pursued by means of (1) a detailed retrospective analysis of reported rabies cases in the study region over several decades, (2) the collection of data on recent (1972-1976) reported rabies cases in the study area, (3) a serum survey to detect rabies antibodies among striped skunks, opossums, and free-roaming domestic cats in the study area using rapid fluorescent focus inhibition test (RFFIT) and serum neutralization (SN) procedures, and (4) an analysis of prominent environmental features and wildlife population characteristics within the study area in relation to the sites of reported rabies cases.

The study found that over approximately three decades the major rabies host shifted from the dog, to the fox, and finally to the skunk. These changes were associated with different spatial and temporal patterns among reported rabies cases. Reported rabies cases occurred in both macrofoci within the study region and microfoci within the study area.

Within the study area reported rabies cases were most numerous during the months of March and April. Microfoci of

reported rabies cases were characterized statistically by areas of low or moderate forest/woodland cover and away from major lakes or rivers. Rabies seropositive opossums, domestic cats, and a striped skunk were found. Approximately 17 percent (101/608) of the opossums sampled were found to be rabies seropositive. The proportion of rabies seropositive opossums increased as the animals matured from juveniles to adults. The salivary gland of one opossum contained rabies antigen. Seropositive opossums and cats were found in most areas where reported rabies cases occurred, but they were distributed over a greater area than reported rabies cases.

The study concluded that clinical rabies within the study region was a dynamic disease entity with changes in host species, spatial pattern, and temporal pattern of reported cases. The microfoci of reported rabies cases in the study area were considered to be real concentration of clinically rabid animals and functions of environmental influences on the host-virus relationship. The temporal focus of reported rabies cases was considered to represent a real peak in clinically rabid animals and may have resulted from the activation of latent rabies infections or newly acquired infections from sources other than clinically rabid animals. Clinical rabies among skunks appeared in an area of low skunk population density. A major decline in the skunk population appeared to precede the rise in reported skunk rabies cases. Rabies infected opossums and cats were dispersed in time and space beyond the spatial and temporal foci of reported rabies cases. These data indicate that the circulation of the rabies virus may not be dependent upon the occurrence of clinically rabid animals. Overall, the study data suggest that the rabies virus may be maintained by nonlethal infections among several species and transmitted by means other than the bite of a clinically rabid animal.

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INTRODUCTION

Rabies has existed as a distinct clinical entity for centuries, and it is certainly one of the worst diseases to plague man and animals. Johnson (1965:815) wrote

> Since antiquity, the period of summer reckoned by the helical rising of the dog star, Sirius, has been referred to as "dog days," when dogs are supposed to be especially liable to spells of madness. It is easy to understand why people of ancient Egypt, Greece, and Rome ascribed the disease to supernatural causes, because animals ordinarily docile and friendly became extremely vicious and aggressive without evident cause . . . .

In 1834 a young British naturalist named Charles Darwin was visiting South America as a crew member of HMS Beagle. While considering the consequences of a recent outbreak of hydrophobia, a once common synonym for rabies, he noted in his diary that

> It is remarkable thus to find so strange and dreadful a disease, appearing time after time in the same isolated spot. It has been remarked that certain villages in England are in like manner much more subject to this visitation than others . . . . In so strange a disease, some information might possibly be gained by considering the circumstances under which it originates in distance climates . . . (Darwin 1839).

It has been almost a century and a half since Darwin pondered the mysterious nature of rabies. During that time monumental progress has been made in elucidating the nature of the causative agent, the clinical effects on individual organisms, and the treatment of the disease in both man and animals. However, Darwin seemed to be wondering why rabid animals occur where they do and when they do. Research directed at answering these two basic ecological questions has only recently been undertaken, and the present study sought to discover new information regarding the factors which influence the time and place at which rabid animals occur.

Clinical rabies is a disease of the nervous system produced by a virus of the family Rhabdoviridae (Fenner and White 1976:410). Many of the clinical aspects of rabies have been well established. These elements include the properties of the rabies virus, the pathogenesis of the virus in the host, and the possible modes of transmission. Other aspects such as the factors influencing the course of infection and the significance of rabies antibodies are not clearly defined. The basic aspects of clinical rabies are presented in Appendix A.

The occurrence of a clinically rabid animal in the wild results from the combined influence of the disease agent, the host animal, and the environment. The interaction of these three elements constitutes the ecological aspects of rabies. Such factors as varying species susceptibility, the focal nature of clinical rabies cases, the role of host species overpopulation in triggering epizootics, the reservoir of the rabies virus, and the correlation of clinical rabies with certain aspects of the annual life cycle of the host are critical elements in the ecology of rabies.

Furthermore, the fact that wildlife rabies data are primarily based on human observations of diseased animals forces a consideration of observed cases in relation to actual cases. These aspects of rabies ecology constituted part of the present investigation. A review of the basic elements of rabies ecology is presented in Appendix B.

A major research tool in the study of wildlife diseases is the serological survey (Appendix C). The use of serological surveys among wildlife populations has increased in recent years. These surveys have permitted the investigation of wildlife diseases by means of serological epizootiology. A large part of the present study centered on a serological survey of three medium-sized mammals in northeastern Tennessee. This survey sought to determine the extent, distribution, and biological characteristics of rabies seropositive animals, animals with rabies antibodies. In addition, this survey provided basic ecological data on these three species. The species sampled were the striped skunk (*Mephitis mephitis*), opossum (*Didelphis virginiana*), and the domestic cat (*Felis domestica*). Basic ecological data and pertinent rabies information are given for the striped skunk in Appendix D, the opossum in Appendix E, and feral domestic cats in Appendix F.

The state of Tennessee is well suited for the study of rabies. While the time of the earliest rabies cases in the state is uncertain, the disease has probably been present in the state since colonial times. Between 1931 and 1940 Tennessee reported 55 human rabies deaths which along with Texas (55 human deaths) represented the highest number of rabies fatalities in any state of the country (Webster 1942: 50-51). During this 10-year period 9.6 percent (55/573) of all human rabies cases in the United States occurred in Tennessee. There were also 4,749 cases of animal rabies reported in Tennessee during this decade (Webster 1942:53). Between 1946 and 1976 there were 24 human rabies deaths in Tennessee which represented slightly less than 10 percent of all human rabies cases in the country (Held et al. 1967: 1014; USDHEW 1976b:9).

Prior to the mid-1950's the available data indicate that rabies in Tennessee was primarily reported in the domestic dog (*Canis familiaris*) (Table 1). In 1953 the state legislature created a Rabies Control Service within the State Health Department, and this service initiated a state-wide dog vaccination program in 1954. By 1955 an estimated 45 percent of the dog population in the state had been vaccinated (Fredrickson 1966:73). In 1955 the decline in dog rabies and a rise in fox rabies resulted in an equal number of reported cases in the two groups. These trends continued into the 1960's and through the explosive fox rabies epizootic of 1964-1968. Except for an upsurge of fox rabies cases during 1972, the number of rabid foxes reported in the state declined gradually during the 1970's.

Table 1. The incidence of reported rabies cases in Tennessee, 1946-1976.

Year	Dog	Cat	Cow	Fox	Skunk	Bat	Other Dom	Other Wild	Man[a]	Total
1946	438	24	24	4	-	-	5	1	1	497
1947	755	42	45	9	-	-	6	-	-	857
1948	623	33	36	15	-	-	6	-	-	713
1949	351	17	22	7	-	-	1	-	-	398
1950	219	8	22	15	2	-	2	-	-	268
1951	286	15	33	31	1	-	3	1	1	371
1952	383	33	38	73	4	-	2	-	1	534
1953	242	37	50	143	4	-	4	1	-	481
1954	125	27	34	96	8	-	14	3	-	307
1955	70	15	23	70	2	-	3	1	1	185
1956	29	5	10	43	7	-	2	2	-	98
1957	21	5	8	32	4	-	1	-	1	72
1958	38	10	23	64	1	-	2	1	-	139
1959	28	6	33	68	4	-	2	1	-	142
1960	31	7	33	99	3	-	7	2	-	182
1961	23	7	42	101	9	2	4	-	-	188
1962	20	10	53	111	17	3	1	-	-	215
1963	27	4	36	53	13	6	1	1	-	141
1964	31	16	68	405	30	13	5	4	-	572
1965	42	22	98	395	72	32	14	9	-	684
1966	33	10	57	194	23	26	10	3	-	356
1967	49	20	51	368	33	18	8	12	-	559
1968	17	10	27	187	19	10	7	4	-	281
1969	9	4	14	60	34	8	-	3	-	132
1970	4	-	5	26	19	10	1	-	-	65
1971	9	9	9	41	31	9	5	1	-	114
1972	19	10	40	100	109	21	11	2	-	312
1973	6	-	25	59	52	6	2	-	-	150
1974	1	-	6	18	20	7	-	1	-	53
1975	-	-	-	5	9	6	1	-	-	21
1976	3	1	1	9	23	11	-	-	-	48
Total	3,932	407	966	2,901	553	188	130	53	5	9,135

[a]Partial data.

Source. Annual Report of Rabies in Tennessee, 1963, 1976, Tennessee Department of Public Health, Nashville, 1964, 1977.

During the 1974-1976 period skunks were the major rabies host in the state. The earliest recorded cases of skunk rabies in Tennessee occurred during 1950. The two rabid skunks in 1950 were located in two nonadjacent counties. One county was on the northern border of middle Tennessee and the other was in the east-central part of the state's interior. From 1950 until 1968 skunk rabies cases were located primarily in middle Tennessee, but in the late 1960's rabid skunks began to occur in eastern Tennessee. There have been few cases of skunk rabies reported in the western part of the state.

In light of the persistent and serious nature of the rabies problem in Tennessee, the present study was undertaken to examine, from an ecological perspective, the environmental factors which may form the basis for this problem and to evaluate the data collected with the aim of proposing procedures which might reduce the incidence of wildlife rabies in the state. The goals of the present study were expressed in the six objectives listed below.

1. The study was to determine whether any major changes occurred in the epizootiology of rabies based upon an analysis of reported rabies cases over the years for which data were available. This analysis was to consider the species composition, spatial distribution, and temporal pattern of reported rabies cases in a multi-county study area in northeastern Tennessee and a zone of surrounding

counties which would constitute the study region.

2. The study was to determine the location of all recent (1972-1976) reported rabies cases within the designated study area in order to establish whether these rabid animals occurred randomly in space or were concentrated in one or more geographical foci. Furthermore, the study was to consider the distribution pattern of reported rabies cases in relation to major environmental features and the distribution of the members of the major host species which were not associated with reported rabies cases. This analysis was to consider the landscape epizootiology of rabies in the study area.

3. The study was to determine the date of all recent (1972-1976) reported rabies cases within the designated study area in order to establish whether these rabid animals occurred randomly throughout the year or were concentrated in one or more temporal foci. If any temporal foci existed, they would be evaluated in relation to the annual life cycle of the major host species in order to consider the factor(s) which might influence the acquisition or reactivation of rabies infections during such period(s).

4. After determining the major host species among reported rabies cases in the study area, the study was to consider the members of this species in two groups. One group would consist of those animals reported as clinical rabies cases. The other group would include all animals of

the species not associated with reported rabies cases. Available data on the age, sex, and distribution of these two groups within the major rabies host species were to be evaluated for significant differences. The study was also to determine, to the extent possible, the relationship between the population dynamics of the major rabies host species and the fluctuations of reported rabies cases in that species. These findings were to be used in analyzing the interrelationship between host population ecology and the incidence of clinical rabies.

5. The study was to determine whether any striped skunks, opossums, and free-roaming domestic cats captured during the study were rabies seropositive. The prevalence of rabies seropositive animals among these species and the age and sex characteristics of rabies seropositive animals within a species would be determined in order to evaluate possible modes of rabies virus maintenance and circulation. Furthermore, the study was to determine the spatial and temporal relationship between rabies seropositive animals and reported rabies cases and consider the epizootiological implications of any such relationships.

6. The study was to evaluate the data from all aspects of the investigation in order to address the fundamental elements of rabies epizootiology. Specifically, the study sought to consider (1) the mean(s) whereby the rabies virus was maintained, (2) the method(s) of viral transmission,

and (3) the factor(s) which might serve to initiate clinical disease following infection by the rabies virus.

CHAPTER I

METHODS AND MATERIALS

I. SELECTION OF THE STUDY AREA AND STUDY REGION

A study area consisting of several counties in northeastern Tennessee was considered appropriate for this investigation of wildlife rabies. The aim was to establish a study area containing both a zone of high rabies incidence and a contrasting zone of low rabies incidence. It was considered desirable to select counties with similar human population densities, topographies, and, if possible, physical continuity.

In early 1973 data published by the Tennessee Department of Public Health on the incidence of laboratory confirmed rabies cases in 12 counties of northeastern Tennessee were summarized for the period between 1969 and 1972 (Fig. 1). These data revealed that during the four-year period Greene County reported the highest incidence of rabies among skunks and all species combined. This county was designated as the area of high rabies incidence. Jefferson and Cocke counties were chosen as the contrasting area of low rabies incidence because the combined area reported only a single case of rabies (cow) in the 1969-1972 period.

In the spring of 1973 the study area was formally established and consisted of three counties divided into two

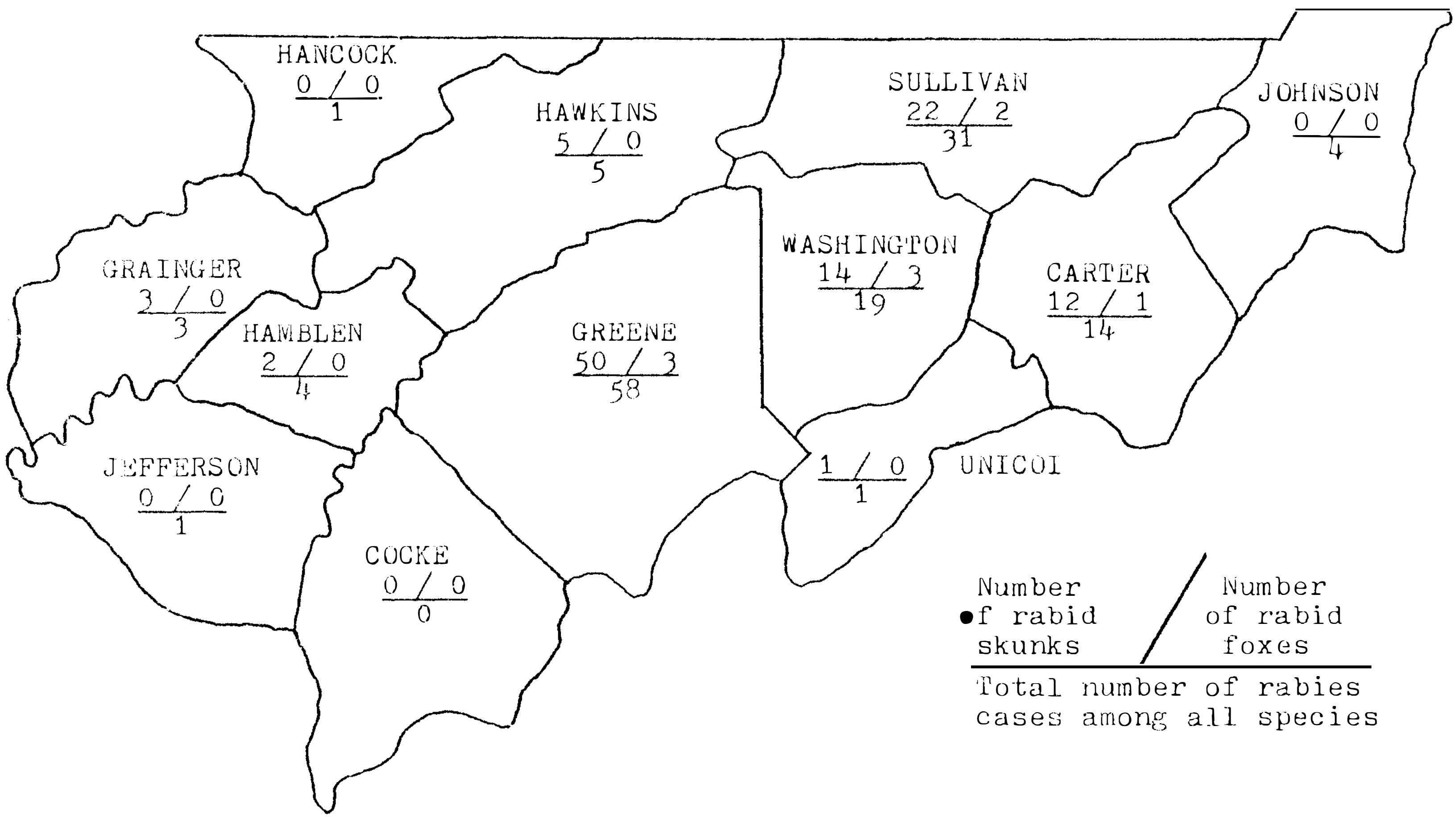


Fig. 1. Results of the preliminary survey of the reported incidence of skunk rabies, fox rabies, and total laboratory confirmed rabies cases in the 12 counties of northeastern Tennessee, 1969-1972. Source: Tennessee Department of Public Health, 1970-1973, Annual Report of Rabies in Tennessee, 1969-1972, Nashville (issued annually).

contrasting zones based on the level of reported rabies (Fig. 2). These three counties form a single continuous land area with similar land use patterns and topography. The total land area and human population of the two zones are similar (Table 2).

In order to put the incidence of rabies cases of the study area in perspective, a larger area, the study region, was established. By considering rabies data of the counties surrounding the study area, any long-term macrofoci and wave-like movements of rabies infection through the region might become apparent. The counties included in the study region were within approximately 60 km of the study area. This criterion produced a study region of 19 counties in eastern Tennessee, eight counties in western North Carolina, and three counties in southwestern Virginia (Fig. 3). The land area, human population, and human population density of the 30 counties in the study region are shown in Table 3.

II. DESCRIPTION OF THE STUDY AREA

The majority of the study area lies within the Great Valley Region of east Tennessee which is located between the Cumberland Plateau on the west and the foothills of the Appalachian Mountains on the east. The general contour of this region is a series of ridges and valleys oriented in a northeast to southwest direction. The remainder of the study area is composed of forested mountains along the Tennessee-

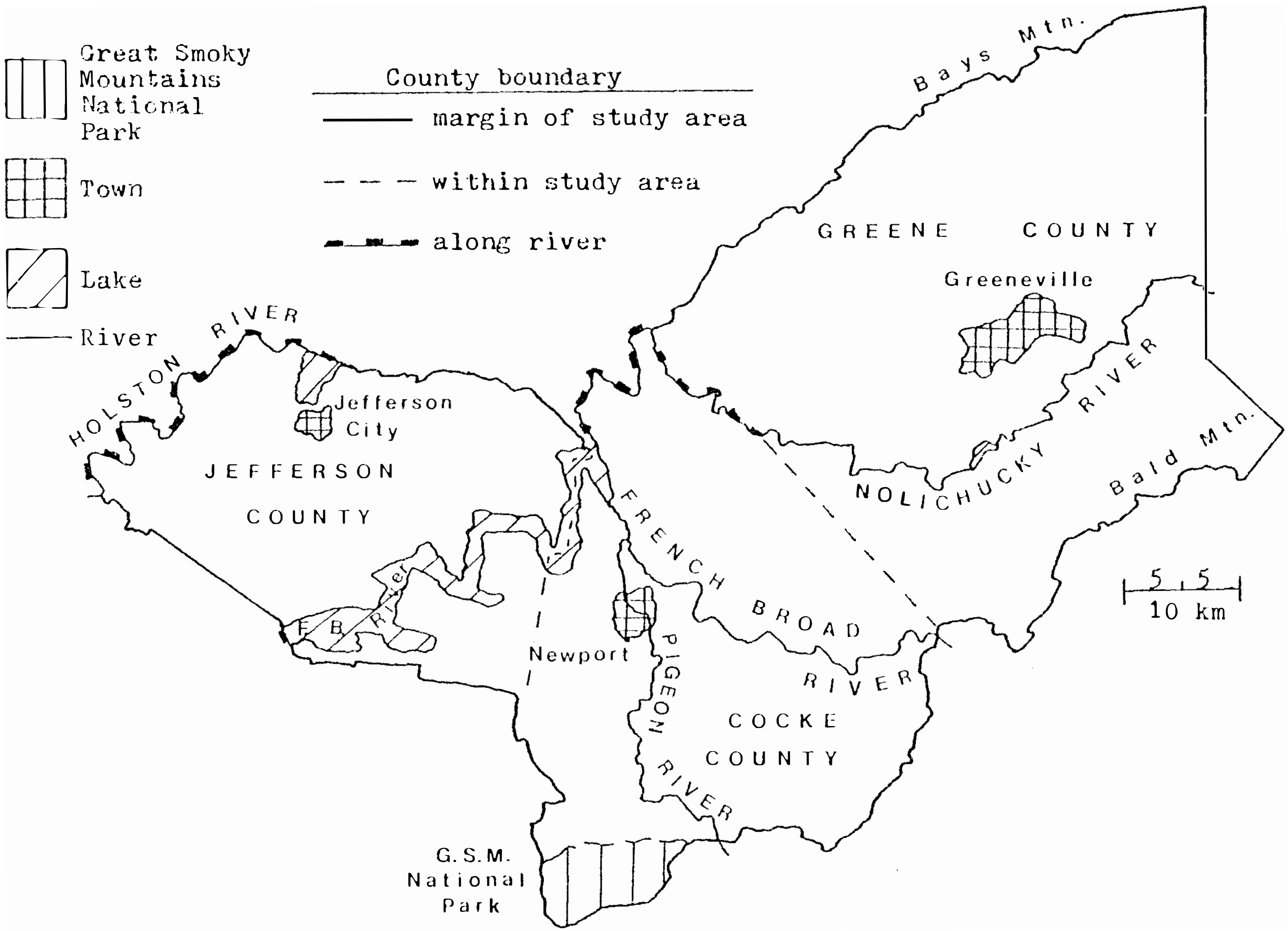


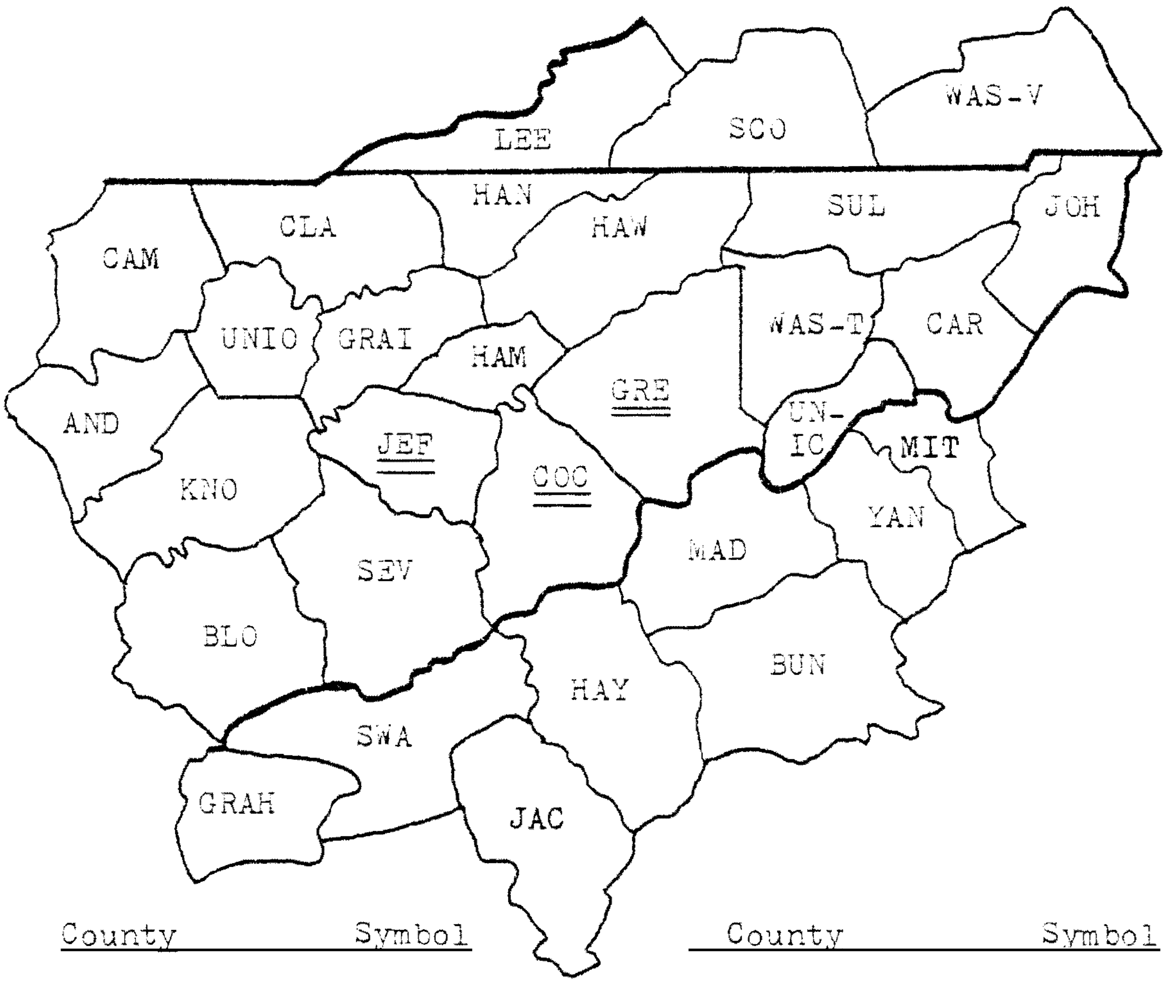
Fig. 2. The three county study area with major geographical features.

Table 2. Land area, human population, human population density, and selected rabies data for the three counties of the study area, the two zones of the study area, and the total study area.

	Designated zone of low rabies incidence			Designated zone of high rabies incidence	Total three county study area
	Jefferson	Cocke	Total	Greene	
Land area[a]					
mi^2	274	424	698	613	1,311
km^2	710	1,098	1,808	1,588	3,396
Population[a] (1970)	24,940	25,283	50,223	47,630	97,853
Population density (persons/km^2)	35.1	23.0	27.8	30.0	28.8
Reported rabies cases[b]					
Foxes (1969-1972)	0	0	0	3	3
Skunks (1969-1972)	0	0	0	50	50
All species (1969-1972)	1	0	1	58	59

[a]Source: U.S. Department of Commerce, Washington, D. C., 1973, County and City Data Book, 1972.

[b]Source: Tennessee Department of Public Health, 1970-1973, Annual Report of Rabies in Tennessee, 1969-1972, Nashville (issued annually).



County	Symbol	County	Symbol
Anderson, Tenn.	AND	Jefferson, Tenn.	JEF
Blount, Tenn.	BLO	Johnson, Tenn.	JOH
Buncombe, N.C.	BUN	Lee, Va.	LEE
Campbell, Tenn.	CAM	Knox, Tenn.	KNO
Carter, Tenn.	CAR	Madison, N.C.	MAD
Claiborne, Tenn.	CLA	Mitchell, N.C.	MIT
Cocke, Tenn.	COC	Scott, Va.	SCO
Graham, N.C.	GRAH	Sevier, Tenn.	SEV
Grainger, Tenn.	GRAI	Sullivan, Tenn.	SUL
Greene, Tenn.	GRE	Swain, N.C.	SWA
Hamblen, Tenn.	HAM	Unicoi, Tenn.	UNIC
Hancock, Tenn.	HAN	Union, Tenn.	UNIO
Hawkins, Tenn.	HAW	Washington, Tenn.	WAS-T
Haywood, N.C.	HAY	Washington, Va.	WAS-V
Jackson, N.C.	JAC	Yancy, N.C.	YAN

Fig. 3. The 30 counties of the study region. Counties with double underline compose the three county study area.

Table 3. Land area, human population, and human population density in the 30 counties of the study region.[a]

County	Symbol	Land area (km^2)	Human population (1970)	Human population density (persons/km^2)
Anderson, Tenn.	AND	868	60,300	69.5
Blount, Tenn.	BLO	1,489	63,744	42.8
Buncombe, N.C.	BUN	1,702	145,056	85.2
Campbell, Tenn.	CAM	1,168	26,045	22.3
Carter, Tenn.	CAR	901	42,575	47.2
Claiborne, Tenn.	CLA	1,150	19,420	16.9
Cocke, Tenn.	COC	1,098	25,283	23.0
Graham, N.C.	GRAH	756	6,562	8.7
Grainger, Tenn.	GRAI	730	13,948	19.1
Greene, Tenn.	GRE	1,588	47,630	30.0
Hamblen, Tenn.	HAM	401	38,696	96.5
Hancock, Tenn.	HAN	596	6,719	11.3
Hawkins, Tenn.	HAW	1,243	33,726	27.1
Haywood, N.C.	HAY	1,427	41,710	29.2
Jackson, N.C.	JAC	1,272	21,593	17.0
Jefferson, Tenn.	JEF	710	24,940	35.1
Johnson, Tenn.	JOH	759	11,569	15.2
Lee, Va.	LEE	1,134	20,321	17.9
Knox, Tenn.	KNO	1,316	276,293	209.9
Madison, N.C.	MAD	1,166	16,003	13.7
Mitchell, N.C.	MIT	557	13,447	24.1
Scott, Va.	SCO	1,396	24,376	17.5
Sevier, Tenn.	SEV	1,546	28,241	18.3
Sullivan, Tenn.	SUL	1,070	127,329	119.0
Swain, N.C.	SWA	1,357	8,835	6.5
Unicoi, Tenn.	UNIC	479	15,254	31.8
Union, Tenn.	UNIO	549	9,072	16.5
Washington, Tenn.	WAS-T	836	73,924	88.4
Washington, Va.	WAS-V	1,487	40,835	27.5
Yancy, N.C.	YAN	808	12,629	15.6
Total		31,559	1,296,075	41.1

[a]Symbols refer to county designations used on Fig. 3, page 30.

Source: U.S. Department of Commerce, 1973, County and City Data Book, 1972, Social and Economic Statistics Administration, 1,020 pp.

North Carolina border. The southern tip of Cocke County is within the Great Smoky Mountains National Park and was excluded from the study area. The Cherokee National Forest encompasses much of southern Cocke and southeastern Greene counties.

The topography of the study area shows much diversity. Jefferson County has a mean elevation between 336 m and 366 m (USDA Soil Survey 1941:3). There are several hilly regions separated by areas designated as plains. The elevated areas are dominated by English Mountain in the southeastern part of the county which rises to an elevation of 1,130 m. Approximately two thirds of Cocke County is in the Great Valley Region which consists of alternating bands of ridges and valleys (USDA Soil Survey 1955:4). The southeastern third of Cocke County lies in the Blue Ridge physiographic province and consists primarily of mountains, sharp-topped peaks, and V-shaped valleys. Elevations within Cocke County range from a low of 305 m on Douglas Lake to over 1,980 m near the southern tip. Most of the ridge tops in the Great Valley Region of Cocke County are approximately 396 m above sea level and 60 to 85 m above the interspersed floodplain (USDA Soil Survey 1955:7). Approximately 80 percent of Greene County is in the Great Valley Region with the remainder composed of mountainous forests (USDA Soil Survey 1958:1). The mountains in Greene County range in elevation from 762 m to 1,476 m above sea level, and the valley floor is approximately 458 m above sea level.

The corresponding physiographic regions of the three counties have similar climates. In the Great Valley Region summers are warm and rather long with the winters cool and moderately short. The mountain regions are cooler and more humid. The winter months which are usually the most critical time for wildlife are characterized by rapid weather changes with short cold periods during which light freezes occur for several nights interspersed among periods of more moderate weather. Snow is not common in the valley region, and the snow which does fall seldom stays on the ground for more than a few days. However, snowfalls are more common in the mountainous areas.

The land in the study area is used primarily for agriculture. Agricultural areas are predominantly cropland, pastures, and woodlots. The amount of land in these and other land use categories is given in Table 4. These data show that Jefferson and Greene counties have similar portions of their areas in cropland, pasture, and forest. Cocke County which contains a part of the Great Smoky Mountains National Park has 44.5 percent of its area in forest.

There are two general types of agriculture practiced in the study area (Martin and Luebke 1960:57, 100-103). The ridge and valley areas of the Great Valley are characterized by tobacco, dairy, and beef farming. Corn is also a major crop. The second type of agriculture is practiced in the

Table 4. Area of the major land use categories (in hectares) in the three counties of the study area, 1967.

	Non agricultural			Agricultural				
County	Federal non farm	Urban, build up	Small water area	Crop-land	Pasture, range	Forest	Other	Total
Jefferson	486	4,452	486	18,050	21,044	23,270	3,197	70,985
% County	0.6	6.3	0.7	25.4	29.6	32.8	4.5	-
% Category	1.3	23.0	29.3	25.3	25.7	20.6	22.2	20.9
Cocke	23,067	2,711	728	17,766	13,638	48,847	3,076	109,833
% County	21.0	2.5	0.7	16.2	12.4	44.5	2.8	-
% Category	60.5	14.0	43.9	24.9	16.7	43.3	21.4	32.3
Greene	14,569	12,222	445	35,573	47,188	40,672	8,134	158,803
% County	9.2	7.7	0.3	22.4	29.7	25.6	5.1	-
% Category	38.2	63.0	26.8	49.8	57.6	36.1	56.4	46.8
Total	38,122	19,385	1,659	71,389	81,870	112,789	14,407	339,621
% Total	11.2	5.7	0.5	21.0	24.1	33.2	4.2	-

Source: Tennessee Statistical Abstract, 2nd ed., 1971, University of Tennessee Center for Business and Economic Research, Knoxville, 712 pp.

mountainous regions of southern Cocke and Greene counties, and is characterized by little commercial agriculture. Croplands are restricted to narrow coves and valleys with tobacco, corn, and hay being the main crops. Data on the number of farms and the average farm size are given in Table 5.

The majority of the human population in the study area lives in a rural setting. Farmers usually live on their farms and thus human dwellings are scattered throughout the area. With the exception of the mountainous areas along the southern and southeastern parts of the study area, little, if any, of the land can be considered as sparsely populated.

While the land in the study area is used primarily for agriculture, over one third of the area is in small woodlands or forest. The study area is included in the Southern Appalachian and Ridge and Valley sections of what Braun (1964:195) refers to as the Oak-Chestnut Forest Region. While the American chestnut (*Castanea dentata*) is no longer found in the area, much of the forest data given by Braun are descriptive of the area today. The forests of the Southern Appalachian section are grouped into three categories. At higher elevations there is a "northern forest" which may include spruce (*Picea* spp.), fir (*Abies* spp.), hemlock (*Tsuga* spp.), yellow birch (*Betula alleghaniensis*), and other northern hardwoods. At lower elevations there is

Table 5. The number of farms, land area in farms, and average farm size for the counties of the study area in 1969 and 1974.

	Jefferson		Cocke		Greene		Total	
	1969	1974	1969	1974	1969	1974	1969	1974
Number of farms	1,691	1,500	1,592	1,305	4,831	3,961	8,114	6,766
Area in farms								
Acres	137,326	119,772	128,219	106,174	321,036	261,766	586,581	487,722
Hectares	55,576	48,472	51,890	42,969	129,923	105,937	237,389	197,381
Average size of farm								
Acres	81	80	81	81	66	66	72	72
Hectares	33	32	33	33	27	27	29	29

Source: U.S. Department of Commerce, 1976, 1974 Census of Agriculture, Preliminary Report (Cocke, Greene, and Jefferson counties), Bureau of the Census, Washington, D. C.

a moist slope and cove forest which contains a mixed mesophytic community with 25 or 30 species, not all of which occur in any one location. The dry slope and ridge forest is composed primarily of oaks (*Quercus* spp.), hickories (*Carya* spp.), and pines (*Pinus* spp.). The Ridge and Valley section contains woodland which are composed primarily of oaks, hickories, and pines. The patchwork nature of woods and fields found in many parts of the study area today is probably beneficial to medium and small-sized mammals.

III. DESCRIPTION OF THE STUDY REGION

The 30 counties of the study region are located in two physiographic provinces (Braun 1964:492-493). The counties in Tennessee and southwestern Virginia are in the southern section of the Ridge and Valley Province which is also known as the Southern Appalachians. This area consists of a series of ridges situated in a northeastern-southwestern orientation and separated by valleys. The area is a mixture of cropland, pastures, and wooded areas. A portion of the Tennessee counties along the North Carolina border and all the counties in North Carolina are in the southern section of the Blue Ridge Province. This area consists primarily of the mountains and foothills of the Appalachian Mountains. Much of this land is covered by forests and cut by swift flowing streams.

IV. RABIES REPORTING IN THE STUDY AREA

Within each county health department of the three counties in the study area, there is at least one individual responsible for rabies control along with other duties. These individuals, known as sanitarians or environmentalists, respond to the calls of county residents who report that they have killed an animal which may be rabid. If this health official believes that the situation warrants a rabies diagnosis of the dead animal, the head of the animal is sent to a regional state laboratory. In Jefferson and Cocke counties these heads are sent to the state laboratory in Knoxville, and the animals from Greene County are sent to the laboratory in Johnson City (Washington County). Both laboratories have essentially the same facilities. Since the number of reported rabies cases has been considered as a function of the distance from a county to the diagnostic laboratory (Prior 1969:35, Lewis 1972:249), it should be noted that the three county health departments of the study area are all less than 80 km from their respective diagnostic laboratory. The travel time from each county health department to the diagnostic laboratory can be less than one hour. In certain cases residents of the study area may carry the head or the entire animal directly to the appropriate state laboratory for a rabies diagnosis. Residents may also carry an animal suspected of having rabies to a local veterinarian who may initiate the submission of the head to either the county health department or the state laboratory. There is no charge for rabies diagnostic work performed by the state.

At the state laboratory the initial test performed on the brain of a rabies suspect is the fluorescent rabies antibody (FRA) test. The principle of the FRA test is given by Kissling (1975:401). Ten slides are made of the brain tissue and tested according to the manual published by the Center for Disease Control entitled "Laboratory Methods for the Detection of Rabies, Course 8260-C." If this test is inconclusive or human exposure is involved, a brain sample is sent to the central laboratory in Nashville for a mouse inoculation test, the basis of which is described by Atanasiu (1975:379).

In all three counties the primary concern in all rabies work is the protection of humans against rabies infection. There is also a concern for valuable domestic animals such as cattle, horses, and hunting dogs. Animals found demonstrating bizarre behavior around these valuable animals are often killed and submitted for rabies diagnosis. Beyond these practical considerations there is very little interest in proving an animal to be rabid in order to monitor the extent of rabies activity in the area. Animals not directly involved with man or domestic animals may not be submitted for a rabies diagnosis despite the distinct appearance of rabid behavior. In general, a rabies diagnosis will be made if it is firmly requested by a county resident regardless of the circumstances.

V. DATA ON ANIMALS SUBMITTED FOR RABIES DIAGNOSIS AND THE INCIDENCE OF LABORATORY CONFIRMED RABIES

Data on the number of laboratory confirmed rabies cases in the counties of Tennessee were obtained from the Tennessee Department of Public Health. The annual report of this department entitled "Rabies in Tennessee" provided data on rabies cases by county and species from 1946 through 1976.

More detailed information regarding the counties of the study area was available at the regional state laboratories in Knoxville and Johnson City. These laboratories supplied current data on both positive rabies cases and those animals which were negative for rabies. These data were further supplemented by information gathered at the county health departments of the three counties. Data collected at the county health departments included the names and addresses of people who submitted animals for rabies examination.

Data on the incidence of reported rabies cases in the North Carolina portion of the study region were supplied by the North Carolina Board of Health in Raleigh. These data covered the period from 1952 through 1976. Data on reported rabies cases in Virginia were supplied by the Department of Health for the Commonwealth of Virginia in Richmond. These data covered the period from 1951 through 1976.

VI. ACCOUNTS OF RABID ANIMALS IN THE STUDY AREA, 1972-1976

In order to gather detailed descriptions of the circumstances surrounding the occurrence of rabid animals during the study, those residents of the study area who submitted animals found to be rabid were interviewed. These interviews were conducted either in person or by telephone. The interview attempted to establish the time of day when the animal was first observed, the behavior of the animal, where the animal was found in relation to the dwelling of the observer, and any interaction between the rabid animal and the other animals in the vicinity. Questions regarding the sex, age class, and general condition of the animal were also asked. Residents were asked about their awareness of the rabies problem in their immediate area and the factors which led them to submit the animal for a rabies diagnosis. The location of each laboratory confirmed rabies case was obtained and plotted on a map of the area for the 1973-1976 period. Data on some rabies cases from 1972 could not be obtained.

VII. COLLECTION OF ANIMALS FOR ECOLOGICAL AND SEROLOGICAL STUDY

Within the study area three species of medium size terrestrial mammals were examined from both an ecological and serological perspective. Data on the striped skunk, the most visible rabies host, were the primary objectives of the study. The opossum, one of the most abundant medium size mammals in the area, was considered to be a potential sentinel species and/or inapparent rabies host. Free-roaming domestic cats which exist to some extent in the truly feral state were sampled only in 1975 for the same reasons as opossums. Although the red fox (*Vulpes vulpes*) and the gray fox (*Urocyon cinereoargenteus*) are found in the study area, both species were omitted from the study because (1) the density of foxes was considered to be too low to provide sufficient data for analyses and (2) reported cases of fox rabies had not occurred in the area for several years.

Data concerning the distribution and population characteristics of the striped skunk and the other animals were based, to varying degrees, on four sources. These sources included (1) interviews relating the account of a rabid animal, (2) the sale of animal pelts by commercial fur trappers in or near the study area, (3) the observation of road-killed animals during all travel in the study area, and (4) the live trapping effort conducted throughout the study area. Serum samples tested for rabies antibodies were collected only from animals captured during live trapping.

In Tennessee fur trappers usually sell their pelts to licensed retail fur dealers located near their homes. These retail fur dealers are required by law to report their purchases (number of pelts by species and trapper) to the Law Enforcement Division of the Tennessee Wildlife Resources Agency. While such data are often fragmentary and a poor index of minor population fluctuations, this information can be used to reveal major, long-term population trends in wildlife populations. The reports submitted by retail fur dealers within and surrounding the study area were examined for such trends.

The date and location of all road-killed striped skunks were recorded during all travel in the study area. Road-killed animals of other species were noted to indicate the presence of these species in the area. No systematic travel was undertaken solely for the purpose of locating road-killed animals, and the extent of observation varied greatly in different parts of the study area.

The live trapping effort was divided into two categories: roadside trapping and farm trapping. Roadside trapping was a widespread, systematic effort to randomly sample animals throughout the study area. Farm trapping was a localized effort on farms where rabid animals had been reported.

Two farms were used during 1974 and eight farms were used during 1976. Each farm site was used only once. The time interval between the occurrence of the rabid animal and trapping varied from 18 to 136 days with an average of 76 days. If the rabid animal was found near a road, traps were normally placed on both sides of the road in a "figure 8" pattern centered on the site. If the site was away from the road, traps were normally placed in a circular or semicircular pattern about the site. The number of trap sites established on each farm depended on the land use and terrain, and the number varied from six to 18 with an average of 12. The distance between trap sites varied from 20 to 50 m.

Roadside trapping constituted the bulk of the trapping effort. Prior to the initiation of field work, the three county study area was divided into 48 trap areas (Fig. 4). This subdivision was used to insure dispersion of the trap effort and to provide a unit of reference for the statistical analyses of data. This subdivision was completed in April 1973, and except for minor alterations, the 48 trap areas remained constant throughout the study. Trap areas in the interior were approximately 8 km square or 64 km^2. Trap areas along the boundaries, in mountainous areas, or near human population centers were adjusted in order to provide an approximately equal amount of trappable area. Trap areas numbered 1 through 24 covered most of Jefferson and Cocke counties, the zone of low rabies incidence (Table 2, page 14).

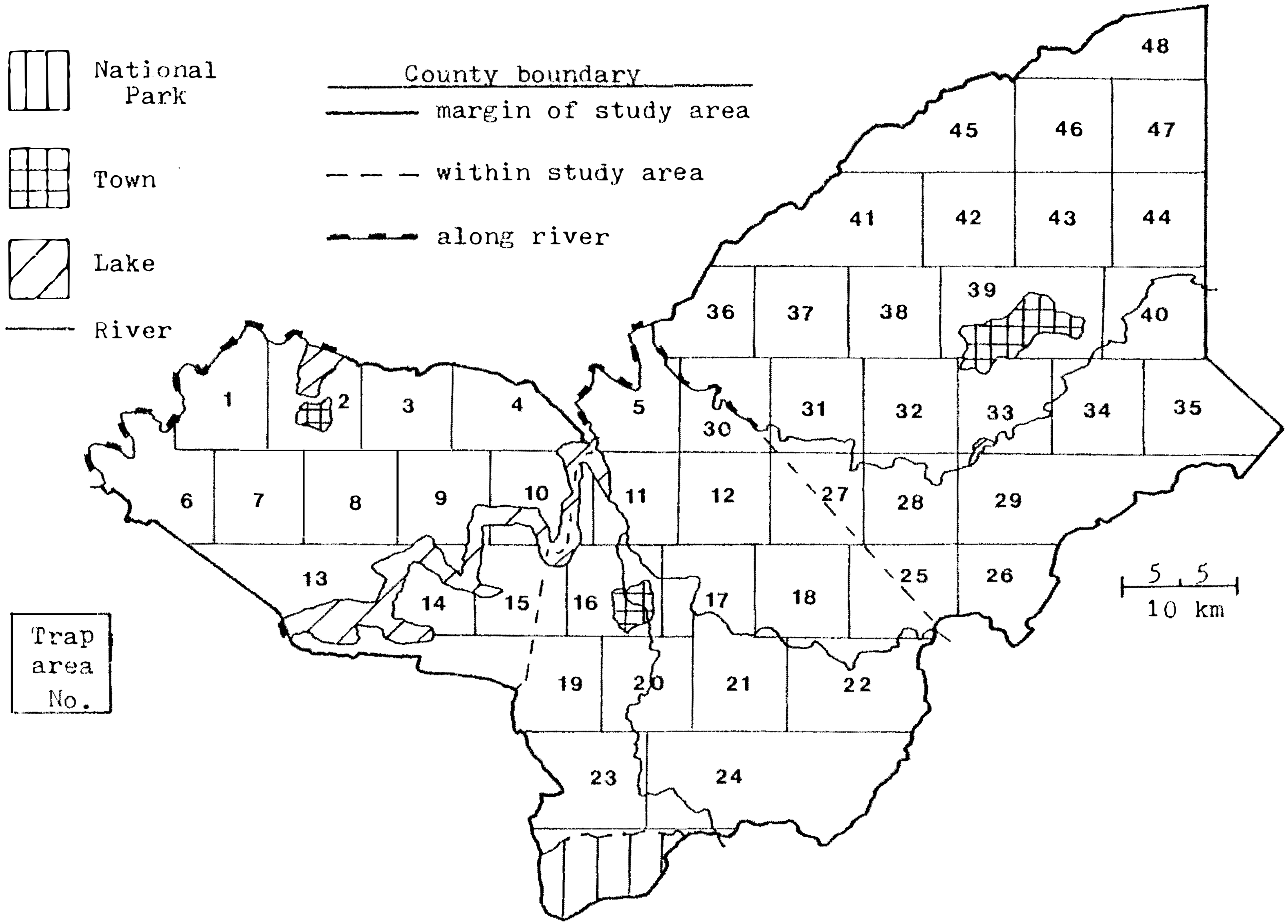


Fig. 4. The three county study area divided into the 48 trap areas.

Trap areas 25 to 48 were composed primarily of Greene County, the zone of high rabies incidence. From 1973 through 1975 each of the 48 trap areas was used at least once in each year. In 1976 only those trap areas near the sites of reported rabies cases or rabies seropositive animals were used.

The trap effort consisted of 48 trap periods (Tables 6 and 7). Except for trap period 10, each period lasted four days with the traps in operation over three nights. In trap period 10 the traps were in operation over only two nights. All data obtained during trap period 19 (27 Feb.-2 March 1974) are considered as occurring in March. Traps were set out on day one, checked once on days two and three, and checked again as they were picked up on day four.

During most of the trap periods, traps were set in four of the 48 trap areas, two trap areas from the 1-24 group and two from the 25-48 group. Initially these four trap areas were randomly chosen and then arranged to provide the shortest travel distance in the field. However, in 1974 the completely random selection of trap areas was abandoned. The use of two trap areas from each of the two groups was continued, but the four trap areas were selected to reduce travel distance and an effort was made to trap an area in the same month during each year of the study.

Each trap area was divided into four quadrants designated by the letters A, B, C, and D. These letters represented

Table 6. Trap periods 1-31 employed during 1973 and 1974 showing the trap areas utilized.

1973			1974		
Number	Dates used	Trap areas	Number	Dates used	Trap areas
1*	May 12-15	3 8 45 48	17	Feb.13-16	4 6 41 42
2*	May 19-22	5 22 34 46	18	Feb.20-23	13 16 40 44
3*	May 26-29	2 11 35 43	19	Feb.27-Mar.2	21 22 25 26
4*	June 11-14	19 21 24 25 27	20	March 4-7	10 12 30 31
5*	June 17-20	4 6 41 42	21	March 19-22	19 20 29 33
6*	June 23-26	13 16 40 44	22	March 24-27	1 7 46 47
7*	July 16-19	7 20 26 29	23	April 1-4	23 24 27 28
8*	July 23-26	12 17 30 31	24	April 8-11	9 14 36 37
9*	July 28-31	10 14 32 33	25	April 17-20	17 18 32 38
10	Aug. 8-10	15 18 28 38	26	April 24-27	8 15 39 43
11	Aug. 14-17	1 9 39 47	27	May 1-4	5 11 34 35
12	Aug. 21-24	23 24 36 37	28	May 6-9	2 3 45 48
13	Sept. 6-9	2 3 45 48	29	May 15-18	4 6 40 44
14	Sept. 11-14	5 8 43 46	30	May 20-23	12 20 29 31 33
15	Sept. 17-20	11 22 34 35	31	June 1-4	1 6 Farm C Farm K
16	Oct. 25-28	13 20 21 25 27			

* = Trap periods without collection of serum samples.

Table 7. Trap periods 32-48 employed during 1975 and 1976 showing the trap areas utilized.

1975			1976		
Number	Dates used	Trap areas	Number	Dates used	Trap areas
32	May 12-15	2 3 45 48	44	July 17-20	Farm B Farm GO Farm GR Farm M Farm V
33	May 17-20	5 11 34 35			
34	May 27-30	4 10 40 44			
35	June 3-6	1 6 41 42	45	July 24-27	Farm F Farm H Farm W
36	June 11-14	19 20 29 33			
37	June 21-24	23 24 25 26	46	Aug. 7-10	45 46 47 48
38	July 19-22	12 16 30 31	47	Aug. 14-17	34 35 39 40 43 44
39	July 26-29	14 15 36 37			
40	Aug. 23-26	8 9 46 47	48	Aug. 26-29	1 2 10 11 16
41	Sept. 3-6	7 13 39 43			
42	Sept. 9-12	21 22 27 28			
43	Sept. 16-19	17 18 32 38			

the northwestern, northeastern, southwestern, and southeastern portion of the trap area, respectively. The first time a trap area was used, two quadrants were selected for trapping and approximately six trap sites were established in each quadrant. The second time the trap area was used the remaining two quadrants were trapped. During the third and subsequent use of the area, an effort was made to use two or three sites from each of the four quadrants. Some trap areas in mountainous areas or near human populations centers could not be divided into equal quadrants, but these trap areas were divided into four sections of irregular shape. After the quadrants in the trap areas had been selected, county road maps were used to determine the most suitable roads for setting out traps.

Traps were set along highway right-of-ways. In general, secondary roads with little traffic were used, but larger four-lane highways were also utilized. Traps were normally set 2 to 20 m off the roadway. The standard procedure was to set 12 traps in each area, and an effort was made to set these traps in a straight line at intervals ranging from 160 to 640 m. However, this procedure could not be followed at all times, and some traps were separated by distances up to 2.5 km. Trap sites were predominantly small woodlots, tall grass fields, fencerows by cropland, and old fields with young trees. An effort was made to place traps near streams and at the interface of two habitat types such as woods and fields or cropland and woods. Approximately 48 traps were used during each trap period, but losses and additions caused slight variations from period to period.

All trapping was done with live traps, and two sizes of traps were used. The majority of the traps were metal wire, single entrance, spring closing, and measured 48 cm x 15 cm x 15 cm. The other traps were similar in design, but measured 51 cm x 19 cm x 19 cm. The bait used throughout the study consisted of a mixture of sardines and a moist, fish-flavored cat food. Approximately 50 to 100 g of bait was kept in each trap during operation.

During the study 1,474 different trap sites were established and operated for a total of 6,632 trap nights (Table 8). There were 1,358 roadside trap sites and 116 farm sites. Of these 1,474 trap sites, 808 sites (54.8 percent) were used in only a single year, 480 sites (32.6 percent) were used in two years, 148 sites (10.0 percent) were used in three years, and 38 sites (2.6 percent) were used in all four years of the study.

In general, the trap sites were well dispersed throughout the study area. In trap areas 1-24 there were 708 different trap sites (Fig. 5) which were used a total of 1,137 times for 3,222 trap nights. In trap areas 25-48 there were 766 different trap sites (Fig. 6) which were used a total of 1,222 times for 3,410 trap nights. In Figs. 5 and 6 the distance between closely spaced sites is necessarily

Table 8. Summary of the trapping effort in the study area, by trap area (TA), 1973-1976.

Trap area (TA)	1973	1974		1975		1976		Total		
	New	New	Repeat	New	Repeat	New	Repeat	Trap periods in area	Trap nights	Different sites
1 (Road)	34/12	73/20	15/5	0	37/13	0	29/9	5	186	32
(Farm C)	-	48/16	0	-	-	-	-	1	48	16
(Farm K)	-	48/18	0	-	-	-	-	1	48	18
2	72/24	9/3	27/9	0	33/11	0	15/5	5	156	27
3	72/24	11/4	25/9	0	42/15	-	-	4	150	28
4	36/12	56/17	17/6	0	34/13	-	-	4	143	29
5	72/27	33/11	3/1	0	31/12	-	-	4	139	38
6	36/12	54/17	21/7	0	38/14	-	-	4	149	29
7	36/13	36/12	0	1/1	35/13	-	-	3	108	26
8	72/24	14/5	21/7	8/3	28/10	-	-	4	143	32
9	35/12	36/12	0	0	35/13	-	-	3	106	24
10	36/12	38/13	0	0	39/14	0	28/10	4	141	25
11	71/24	12/4	24/8	0	37/13	0	18/6	5	162	28
12	36/12	48/17	15/5	0	35/12	-	-	4	134	29
13	70/24	11/4	25/9	3/1	32/11	-	-	4	141	29
14	36/12	24/9	8/3	0	36/12	-	-	3	104	21
15	24/12	36/13	0	0	36/12	-	-	3	96	25
16	36/12	35/12	0	6/2	28/10	0	15/5	4	120	26
17	36/12	36/12	0	3/1	32/11	-	-	3	107	25
18	24/12	32/11	6/2	0	30/11	-	-	3	92	23
19	36/12	28/12	6/2	0	30/13	-	-	3	100	24
20	48/16	37/13	31/11	0	40/14	-	-	4	156	29
21	35/14	36/13	0	7/3	26/12	-	-	4	104	30
22	72/26	16/9	20/7	1/1	34/14	-	-	4	143	36
23	36/12	36/13	0	0	35/14	-	-	3	107	25
24	60/22	35/12	4/2	0	40/14	-	-	3	139	34

Table 8. continued.

Trap area (TA)	1973 New	1974 New	1974 Repeat	1975 New	1975 Repeat	1976 New	1976 Repeat	Total: Trap periods in area	Total: Trap nights	Total: Different sites
Subtotal TA 1-24	1,121/394	782/268	268/93	29/12	823/301	0	103/35		3,222	708
Annual total TA 1-24	1,121/394	1,146/395		852/313		103/35			3,222	708
25	71/26	15/5	21/7	1/1	36/13	-	-	4	144	32
26	36/12	11/6	24/8	3/2	29/10	-	-	3	103	20
27	72/24	23/8	15/5	6/3	29/12	-	-	4	145	35
28	24/12	37/13	0	4/2	27/9	-	-	3	92	27
29	36/14	48/12	18/6	0	35/13	-	-	4	137	26
30	36/12	39/13	0	3/1	32/12	-	-	3	110	26
31	36/12	53/16	15/5	0	39/13	-	-	4	143	28
32	35/12	36/13	0	0	34/12	-	-	3	105	25
33	35/13	52/17	12/4	0	33/13	-	-	4	132	30
34	73/26	12/4	26/8	0	30/12	0	3/1	5	144	30
35 (Road)	75/27	6/2	27/9	0	35/13	0	32/11	5	175	29
(Farm F)	-	-	-	-	-	39/14	0	1	39	14
36	35/13	37/14	0	1/1	32/12	-	-	3	105	28
37	33/13	37/13	0	0	43/15	-	-	3	113	26
38	22/11	34/13	0	0	36/12	-	-	3	92	24
39	36/13	28/10	9/3	9/3	28/8	0	9/3	4	113	26
40 (Road)	36/12	63/20	9/3	0	35/13	0	25/9	5	169	32
(Farm W)	-	-	-	-	-	34/12	0	1	34	12
41	36/12	32/14	0	2/2	31/12	-	-	3	101	28
42	36/12	35/12	0	1/1	34/15	-	-	3	106	25
43	69/26	19/7	15/5	6/2	33/11	0	9/3	5	151	35

Table 8. continued.

Trap area (TA)	1973 New	1974 New	1974 Repeat	1975 New	1975 Repeat	1976 New	1976 Repeat	Total: Trap periods in area	Total: Trap nights	Total: Different sites
44 (Road)	36/12	53/18	12/4	3/1	34/12	0	35/13	5	173	31
(Farm B)	-	-	-	-	-	18/6	0	1	18	6
(Farm H)	-	-	-	-	-	39/14	0	1	39	14
(Farm M)	-	-	-	-	-	22/9	0	1	22	9
45	71/25	8/3	30/10	2/1	36/12	0	27/9	5	174	29
46 (Road)	71/25	21/8	12/5	0	32/12	0	26/11	5	162	33
(Farm GR)	-	-	-	-	-	26/10	0	1	26	10
47 (Road)	34/12	36/13	0	5/3	28/11	0	29/10	4	132	28
(Farm V)	-	-	-	-	-	23/9	0	1	23	9
(Farm GO)	-	-	-	-	-	22/8	0	1	22	8
48	70/24	10/4	25/9	8/3	27/10	0	27/8	5	167	31
Subtotal TA 25-48	1,114/400	745/258	270/91	54/26	782/287	223/82	222/78		3,410	766
Annual total TA 25-48	1,114/400	1,015/349		836/313		445/160			3,410	766
Annual total TA 1-48	2,235/794	2,161/744		1,688/626		548/195			6,632	1,474

[a]Data show number of trap nights/number of trap sites used. "New" refers to the first year of use for a site; "Repeat" refers to the second, third, or fourth year of use for a site. - = Area not used during year.

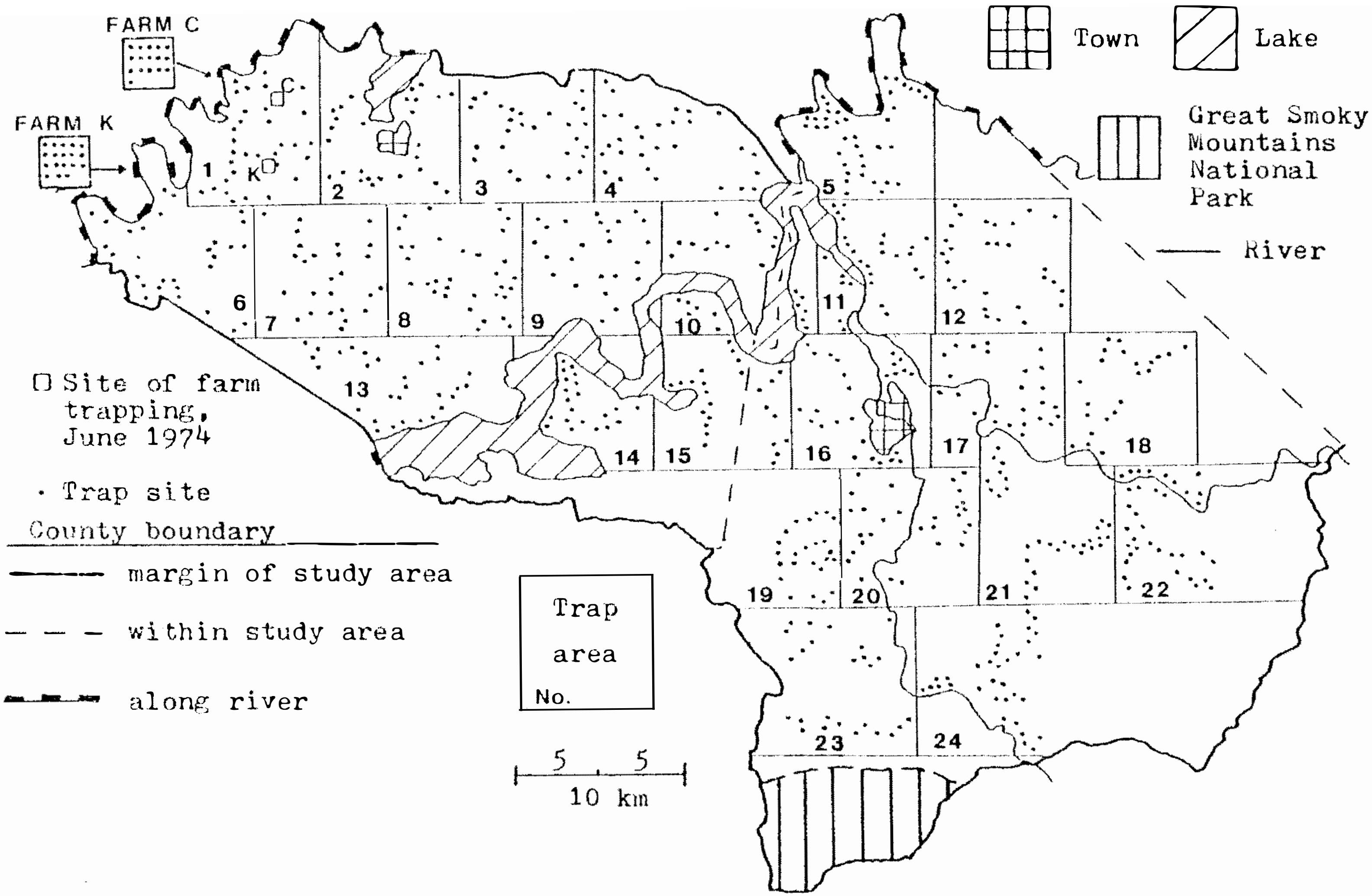


Fig. 5. Distribution of the 708 trap sites used in trap areas 1-24, 1973-1976.

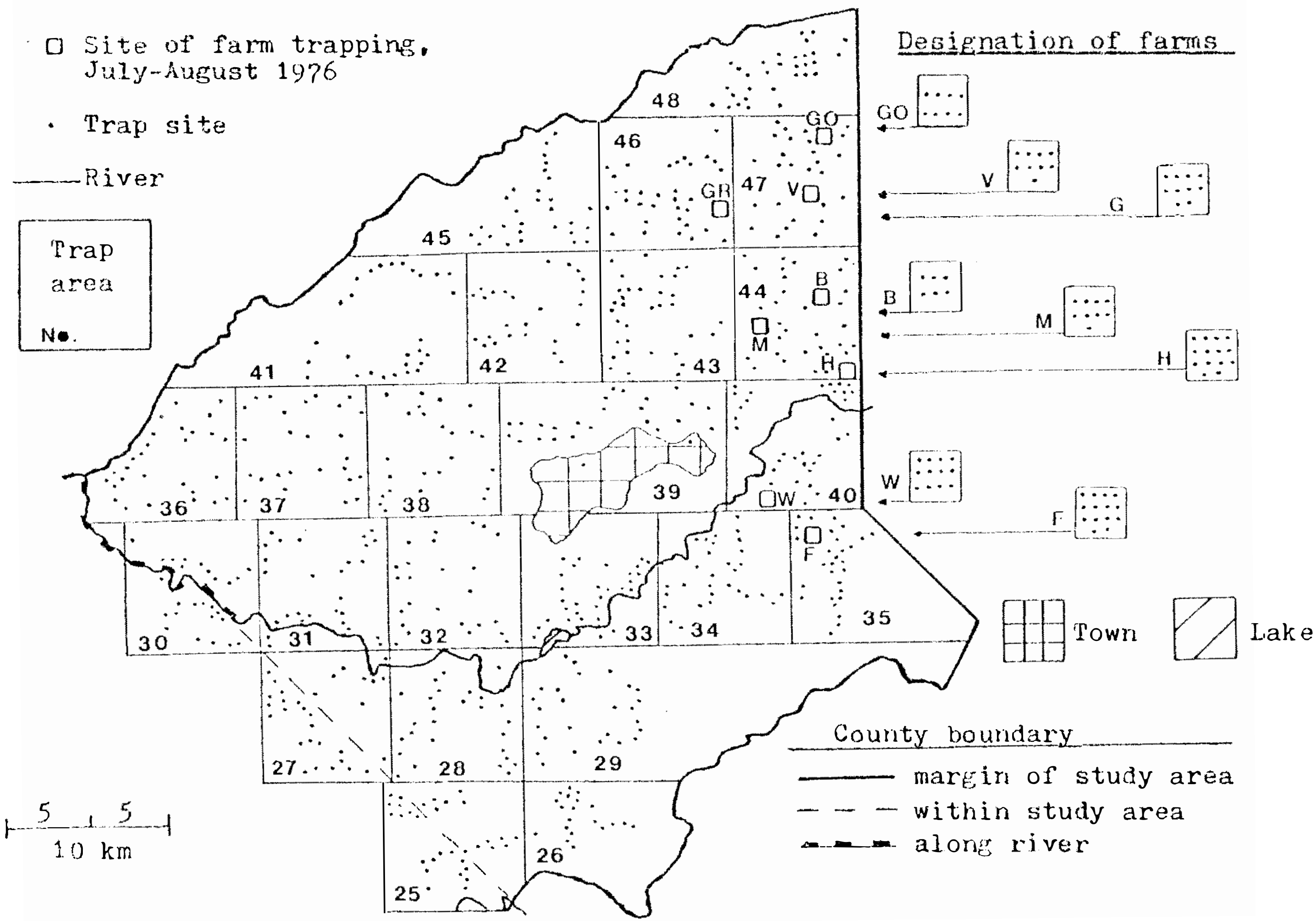


Fig. 6. Distribution of the 766 trap sites used in trap areas 25-48, 1973-1976.

exaggerated to maintain clarity. While the dispersion of trap sites shown on these figures is slightly exaggerated, these representations do give a basic understanding of the extensive area utilized during the trap effort.

VIII. COLLECTION AND ANALYSIS OF BLOOD FOR RABIES ANTIBODIES

When striped skunks were captured, the entire trap was moved on a long aluminum pole and placed in a plastic garbage bag into which a chloroform soaked rag was added. Opossums could usually be carried by hand from the trap site and placed in a second trap already in the garbage bag. Free-roaming cats were anesthetized with an intramuscular injection of ketamine hydrochloride at a dose rate of 0.1 ml/ 454 g of body weight.

After the animal was anesthetized, it was placed in a dissecting pan. At this time data were collected on the sex, weight, body measurements, and any outstanding physical abnormalities of the animal. With female opossums the presence or absence of pouch young was recorded. A blood sample of approximately 10 ml was taken by means of cardiac puncture. Disposable needles and syringes were used in all blood collection. The blood samples were placed in evacuated glass tubes and allowed to clot. On returning to the laboratory the blood tubes were spun in a centrifuge, and the serum poured into smaller plastic tubes. These serum tubes were stored at -18° C. The serum samples were periodically transported on dry ice to the Rabies Control Unit at the Lawrenceville Facility of the Center for Disease Control in Lawrenceville, Georgia. After sampling, striped skunks and opossums were killed with an overdose of chloroform, collected, and stored for use in other studies. Cats were allowed to recover and were released.

All serum analyses were performed by the personnel of the Viral Zoonoses Laboratory of the Center for Disease Control in Lawrenceville, Georgia. An outline of the serum analysis procedure is given in Fig. 7. All serum samples were initially tested by the rapid fluorescent focus inhibition test (RFFIT) (Smith et al. 1973). This test involved the addition of a cell suspension to a rabies challenge virus-serum sample mixture. If rabies neutralizing antibodies were present in the serum, there was a reduction in the number of cells infected by the virus. After 24 hours the cell culture was tested by the fluorescent antibody procedure to determine the extent of rabies infection. The results were observed under a fluorescent microscope using the procedure given by Smith et al. (1973:536).

> Twenty low power (160X) microscope fields are observed for each of the 8 Lab-Tek dilution chambers, and the number of fields containing fluorescent cells are tabulated. Of the 20 fields observed in the challenge virus control slides, 18-20 contain fluorescing cells . . . . A reduction of 50% or more in the number of fields with fluorescing cells . . . indicates the presence of neutralizing antibodies in the test serum.

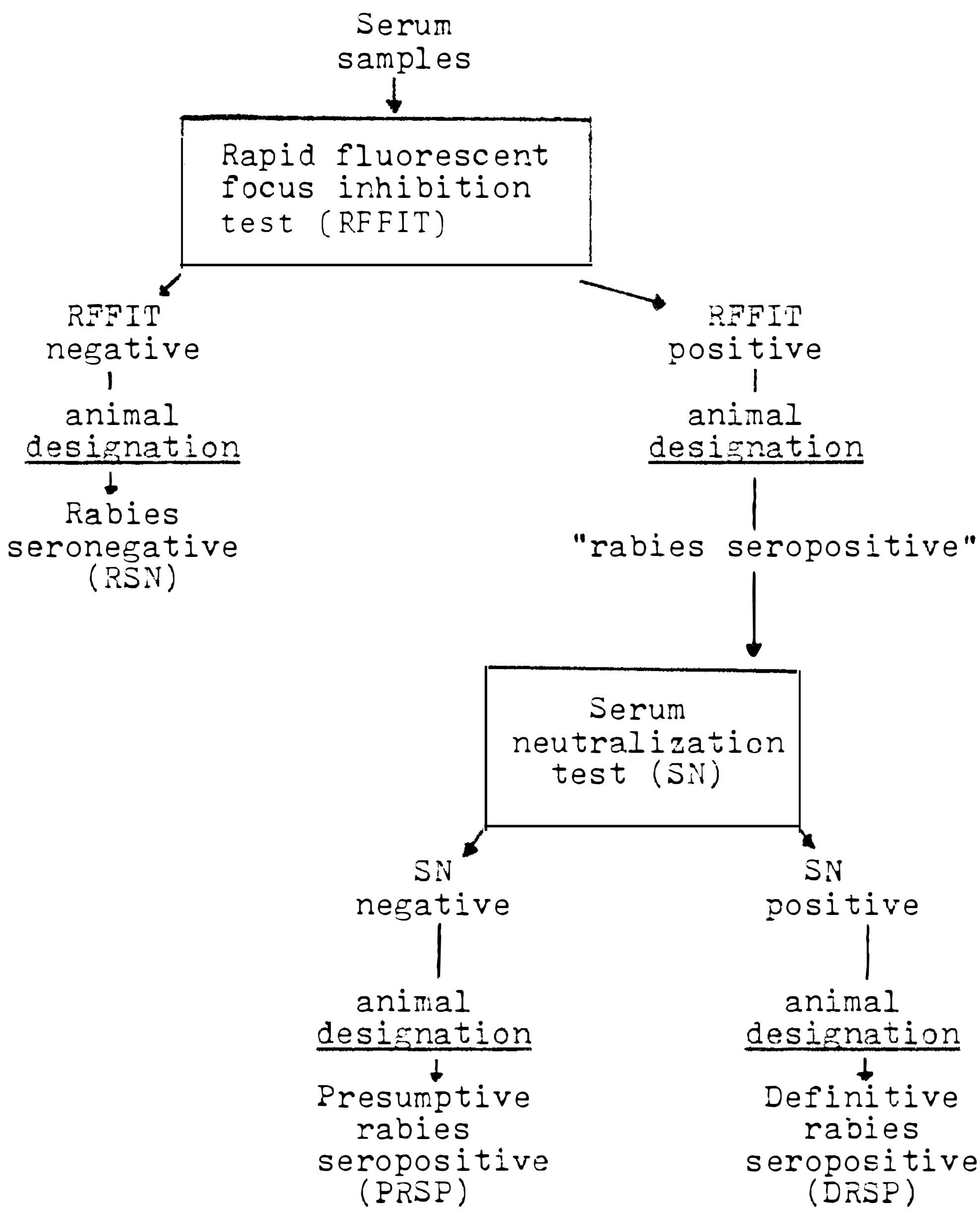


Fig. 7. Diagram of serum analysis procedure and the terminology used for animals sampled during the serum survey.

Such a reduction in the infection of the cell culture by the rabies virus at a serum dilution of 1:5 was considered to be presumptive evidence that rabies antibodies were present in the serum sample. Those serum samples which were RFFIT positive were then tested by the serum neutralization (SN) test according to the procedure of Atanasiu (1973: 314-318). In this test undiluted serum was mixed with an equal volume of a rabies challenge virus suspension, and this mixture was inoculated intracranially into five young mice. If three or more mice failed to develop rabies, the serum was considered to contain rabies serum neutralizing antibodies. The SN test is also known as the virus neutralization (VN) test and the mouse inoculation (MI) test.

There was a close agreement among the results of human sera tested by both the RFFIT and VN test. Among 512 human sera tested there was a 95 percent (487/512) agreement between the two procedures. The RFFIT showed positive results in 5 percent of the cases where the VN test was negative (Smith et al. 1973:536, 539). Among 10 dogs vaccinated against rabies, there was a qualitative agreement in nine cases between the RFFIT and the VN test, but in one animal the RFFIT titer was 1:11 and the VN titer was less than 1:5 (Smith et al. 1973:539).

There are no precise quantitative data regarding the occurrence of false positives (positive test results based on inhibitory sustances not elicited by the rabies virus) with the RFFIT procedure in serological surveys among wildlife populations. The possibility naturally exists that a portion of the animals designated as rabies seropositive had not been exposed to the rabies virus. Smith et al. (1973:535) stated that approximately 10 percent of all normal animal sera may have nonspecific inhibitors of rabies virus at low dilutions, and such inhibitors may have occurred at higher or lower frequencies among the animals tested in this survey. The serum analysis in this study did not include a kaolin treatment of the serum samples prior to testing.

In addition to the occurrence of false positives, the existence of false negatives must also be considered. False negatives would be those animals which had been exposed to rabies and failed to develop detectable rabies antibodies. Barr (1961:59-60) found that only 17.6 percent (3/17) of the opossums inoculated intracranially with a potentially lethal dose of rabies virus produced detectable rabies antibodies. In determining the distribution of the rabies virus in the study area, the problem of false negatives is perhaps of greater concern than the existence of false positives.

Those animals whose sera were positive by the RFFIT were designated by the general term rabies seropositive. The animals whose sera gave presumptive indications of rabies antibody presence by the RFFIT, but were subsequently found negative by the SN test were designated as presumptive rabies seropositive (PRSP). Those animals whose sera were positive by both the RFFIT and the SN test were considered to be definitive rabies seropositive (DRSP).

The RFFIT is considered to be a more sensitive procedure than the SN test (Smith et al. 1973:536, 539). The former may be able to detect low levels of antibodies which might be missed by the SN test. Therefore, PRSP animals should not be regarded, a priori, as containing a large percentage of false positives. These animals may have been exposed to a very small dose of the rabies virus and/or been exposed many months or years before sampling.

In this study the probability that most of the animals found to be rabies seropositive had actually been exposed to the rabies virus was considered sufficient for this ecological investigation. Rabies seropositive animals were considered to be individuals which had been exposed to the rabies virus, but no attempt was made to characterize the nature of the infection, e.g., latent, chronic carrier, or clinically ill. Because the nature of the study was primarily ecological, a qualitative analysis of each sample was considered sufficient. In most cases the designation of an animal as PRSP or DRSP was made without a determination of the exact rabies antibody titer in the serum.

IX. COLLECTION AND ANALYSIS OF SALIVARY GLANDS FOR RABIES VIRUS

In 1975 and 1976 a sample of salivary gland tissue was collected in the field from each striped skunk and opossum captured. This sample consisted primarily of the submandibular and/or parotid gland. The sample was removed with sterile forceps and scissors, and placed in a plastic tube. These tubes were placed in a tight sealing plastic food container which was wrapped in three separate plastic bags. The container was then placed in a styrofoam chest containing dry ice. On returning to the laboratory the samples were transferred to a special freezer which maintained the samples at -70° C.

After the serum analysis was completed by the Center for Disease Control, the salivary gland sample from definitive rabies seropositive, presumptive rabies seropositive, and some rabies seronegative animals (controls) were selected for fluorescent rabies antibodies (FRA) testing to determine whether the animal may have been shedding rabies virus in its saliva at the time of capture. All FRA testing was done by Ed Miller at the regional state laboratory in Knoxville during December, 1976. The procedure was the same as that used for brain tissue submitted for routine rabies diagnosis except that only two slides were made for each salivary gland tissue sample.

Those tissue samples which were positive for rabies antigen by the FRA test were submitted to the main state laboratory in Nashville for a mouse inoculation test in order to demonstrate conclusively the presence of infective rabies virus.

X. DETERMINATION OF ENVIRONMENTAL FACTORS AND THE ESTABLISHMENT OF A HABITAT INDEX

The major environmental factors which were evaluated in relation to reported rabies cases were taken directly from U.S. Geological Survey topographic maps with a scale of 1:24,000. These factors included caves, rivers, lakes, and human population centers. The location of caves was also based on data given by Barr (1961) and Matthews (1971). Approximately 25 maps covered the bulk of the study area. The majority of these maps were based on data gathered in the 1960's, but some had been revised in the 1970's and a few were based on data from the 1939-1940 period. However, the data on the maps were considered adequate for comparing different parts of the study area.

In order to determine the proportion of forest/woodland cover and open land in each of the 48 trap areas, an index was established which classified each trap area on a scale from 0 (mostly open) to 4 (mostly forest/woodland cover). This index number was determined using a concept similar to that given by Bryant (1943). A transparent sheet divided into 100 grid squares was placed over the topographic map of each trap area. Each grid had 25 small, uniformly spaced dots. Areas on the maps with small woodlots or forest were shaded in green while open areas were white. If five or less dots fell on shaded areas, the grid was given a value of 0. If 6-10 dots fell on shaded areas, the grid was given a value of 1. If 11-15 dots fell on shaded areas, the grid was given a value of 2. If 16-20 dots fell on shaded areas, the grid was given a value of 3. If 21-25 dots fell on shaded areas, the grid was given a value of 4. The sum of the grid values was divided by the number of grids evaluated to give the habitat index of the trap area. While most of the 48 trap areas were evaluated on the basis of approximately 100 grid squares, some variation did occur.

XI. ANALYSIS OF DATA

A major area of statistical consideration was whether certain phenomena were randomly distributed in time and space or clustered in temporal and geographical foci. These phenomena included the location of rabid animals and the sex, age class, and distribution of rabies seropositive animals. In most cases the geographical unit of reference was the trap area. The frequency distribution of these data was compared with the random Poisson distribution using the chi-square goodness-of-fit test as outlined by Gibbons (1976: 36-56).

Another statistical requirement was to determine whether certain aspects under investigation varied in a direct or inverse manner. In these analyses the trap areas or sets of trap areas were ranked in descending order according to one variable and this rank order was compared to the rank order based on a second variable. The Spearman coefficient of rank correlation (Gibbons 1976:275-282) was used to determine whether the two variables were directly (values up to +1) or inversely (values down to -1) related.

A third area of statistical consideration involved finding the degree of association between two sets of data. This effort primarily sought to measure the geographical similarity in the distribution of like data for two different years or two types of data during the same year. The units of geographical reference were either the counties of the study region or the trap areas of the study area. The events being evaluated were either present or absent in each geographical unit. The degree of association again ranged from -1 for totally dissimilar distribution patterns to +1 for completely identical patterns with 0 indicating an independent distribution of the two factors or events. The degree of association was based on the point correlation coefficient (V) as outlined by Poole (1974:336). Two examples showing the determination of this coefficient are given in Fig. 8.

During the study there was no attempt to estimate the population density of the species sampled. The capture rate

A. The use of V in comparing the distribution of reported rabies cases within the 30 county study region for 2 years. This value is a measure of the recurrence of reported rabies cases.

		Reported rabies cases 1962		
		Counties with rabies cases	Counties without rabies cases	
Reported rabies cases, 1976	Counties with rabies cases	5 (cases both years)	3	8
	Counties without rabies cases	6	16 (cases neither year)	22
		11	19	30

$$V = \frac{(5)(16) - (3)(6)}{\sqrt{(8)(22)(11)(19)}} = \frac{80 - 18}{191.8} = \frac{62}{191.8} = +0.323$$

B. The use of V in comparing the distribution of different types of data within the 48 trap areas of the 3 county study area.

		Rabies seropositive opossums, 1975		
		Trap areas with seropos. opossums	Trap areas without seropos. opossums	
Reported rabies cases, 1975	Trap areas with rabies cases	0 (both present)	1	1
	Trap areas without rabies cases	30	17 (both absent)	47
		30	18	48

$$V = \frac{(0)(17) - (1)(30)}{\sqrt{(1)(47)(30)(18)}} = \frac{0 - 30}{159.3} = -0.188$$

Fig. 8. The use of the point correlation coefficient to measure the degree of geographical association between similar types of data for two different years (A) and between different types of data from a single year (B). Values of V range from +1 for identical patterns to -1 for total dissimilarity.

(captures per 100 trap nights) formed the basis for comparing the relative abundance of the animals sampled. The site success rate (the percentage of trap sites used which yielded one or more captures) was used as an index for comparing the dispersal, or distribution, of a species within the geographical unit of reference.

CHAPTER II

RESULTS

I. RABIES IN THE STUDY REGION

During the 31-year period from 1946 through 1976, 3,651 cases of animal rabies were reported in the 30 county study region among 17 animal categories (Table 9). During this period the annual total of reported cases and the species composition of the annual total varied greatly (Table 10). The annual number of reported rabies cases ranged from 367 in 1965 to only three reported cases in 1975.

The largest number of reported rabies cases occurred among foxes followed in descending order by dogs, cattle, skunks, cats, and bats. Some of the animal categories with smaller numbers of reported cases such as the bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), and domestic farm animals are not uncommon victims of rabies in the southeastern United States. However, the occurrence of rabies in an opossum, a deer (*Odocoileus* spp.), a rabbit (*Sylvilagus* spp.), and rodents such as a muskrat (*Ondatra zibethicus*) and a woodchuck (*Marmota monax*) are rare throughout the United States.

Annual rabies cases among cattle and cats did not fluctuate widely and occurred regularly in the study area prior to the 1970's. While cattle represented almost 12 percent of all reported rabies cases, this group is not

Table 9. Total incidence of laboratory confirmed rabies cases among various animal categories in the 30 county study region.

Animal category	Rabies cases	Percentage
Dog	1,388	38.0
Cat	166	4.5
Cow	429	11.8
Fox	1,409	38.6
Skunk	181	5.0
Bat	22	0.6
Other, domestic animals		
Horse	9	0.2
Mule	4	0.1
Swine	4	0.1
Sheep	4	0.1
Other, wildlife		
Bobcat	10	0.3
Raccoon	3	0.1
Deer	3	0.1
Muskrat	1	*
Opossum	1	*
Rabbit	1	*
Woodchuck	1	*
Unspecified	15	0.4
Total	3,651	

*Less than 0.05 percent. Tennessee counties, 1946-1976; Virginia counties, 1951-1976; North Carolina counties, 1952-1976.

Table 10. Annual incidence of laboratory confirmed rabies cases among major animal categories in the 30 county study region, 1946-1976.

Year	Dog	Cat	Cow	Fox	Skunk	Bat	Other	Total
1946[a]	127	8	9	-	-	-	4	148
1947[a]	229	10	13	2	-	-	1	255
1948[a]	239	16	16	9	-	-	7	287
1949[a]	84	5	8	2	-	-	-	99
1950[a]	49	1	6	9	-	-	1	66
1951[b]	148	6	18	2	-	-	-	174
1952	218	17	14	22	-	-	1	272
1953	95	9	10	32	1	-	1	148
1954	38	8	8	19	-	-	2	75
1955	23	5	11	16	-	-	-	55
1956	7	1	3	17	-	-	-	28
1957	11	2	9	65	-	-	-	87
1958	18	6	21	56	-	-	3	104
1959	9	2	13	45	1	-	1	71
1960	19	5	19	57	-	-	2	102
1961	5	4	20	88	2	-	1	120
1962	11	5	30	56	-	-	3	105
1963	2	1	4	15	-	2	-	24
1964	10	6	26	228	1	-	1	272
1965	12	17	53	273	3	1	8	367
1966	10	9	36	109	4	2	6	176
1967	11	10	31	129	3	2	5	191
1968	3	5	14	48	-	2	3	75
1969	2	5	23	51	35	2	3	121
1970	4	-	9	47	14	3	-	77
1971	1	3	1	5	8	1	-	19
1972	1	-	4	3	70	5	2	85
1973	-	-	-	1	9	-	-	10
1974	-	-	-	-	10	1	-	11
1975	-	-	-	-	2	-	1	3
1976	2	-	-	3	18	1	-	24
Total	1,388	166	429	1,409	181	22	56	3,651

[a]Data for 19 Tennessee counties only.

[b]Data for 19 Tennessee and 3 Virginia counties only.

considered to be a significant reservoir or vector of the rabies virus. The number of cattle rabies cases paralleled, to some extent, the fluctuations of rabies cases in the carnivorous rabies hosts. Therefore, cattle rabies cases were not considered in seeking an epizootiological interpretation of the reported rabies cases within the study region.

While the severity of the animal rabies problem varied over the years considered, the fact that some clinically rabid animals were reported during each year attests to the persistence of the virus in the study region. The rabies history of the study region was examined for major trends. These trends involved (1) changes in the species composition of reported cases between years and (2) changes in the spatial pattern of reported cases. Appendix G presents maps of the study region which show the geographical distribution of reported rabies cases among dogs, foxes, skunks, and all species in four-year units from 1946 through 1969 and for individual years from 1970 through 1976.

Changes occurred in the animal category which constituted the major rabies host (the animal category with the largest number of reported cases in the year) (Table 10). Over the 31 years examined, three animal categories served as the major host of reported rabies in the study region. Each animal category assumed this role during a distinct, uninterrupted period of time. The dog was the major rabies host from 1946, the year of the earliest records, through 1955. The fox was the major rabies host from 1956 through 1970. The skunk was the major rabies host from 1971 through the termination of the study in 1976. The relationship of reported rabies cases among these three animal categories during the 1946-1976 period is presented in Fig. 9.

One aspect of the spatial pattern of reported rabies cases was the number of counties which reported rabid animals. Over the 31 years considered, the number of counties which reported rabies cases appeared to decline in a gradual, but uneven, manner (Table 11). During the 1952-1955 period, data were available for all 30 counties and the dog was the major rabies host. During these four years rabid dogs were reported in an average of 12.5 counties per year, and rabid animals of all species occurred in an average of 15.2 counties per year. During the period characterized by fox rabies, 1956-1970, rabid foxes were reported in an average of 9.3 counties per year. During this 15-year period rabid animals of all species were reported in an average of 11.9 counties per year. The period from 1971 through 1976 was characterized by skunk rabies and showed the smallest geographical extent of reported cases. During these six years rabid skunks were reported from an average of 5.2 counties per year, and rabid animals of all species were reported in an average of 7.2 counties per year.

The apparent reduction in the number of counties

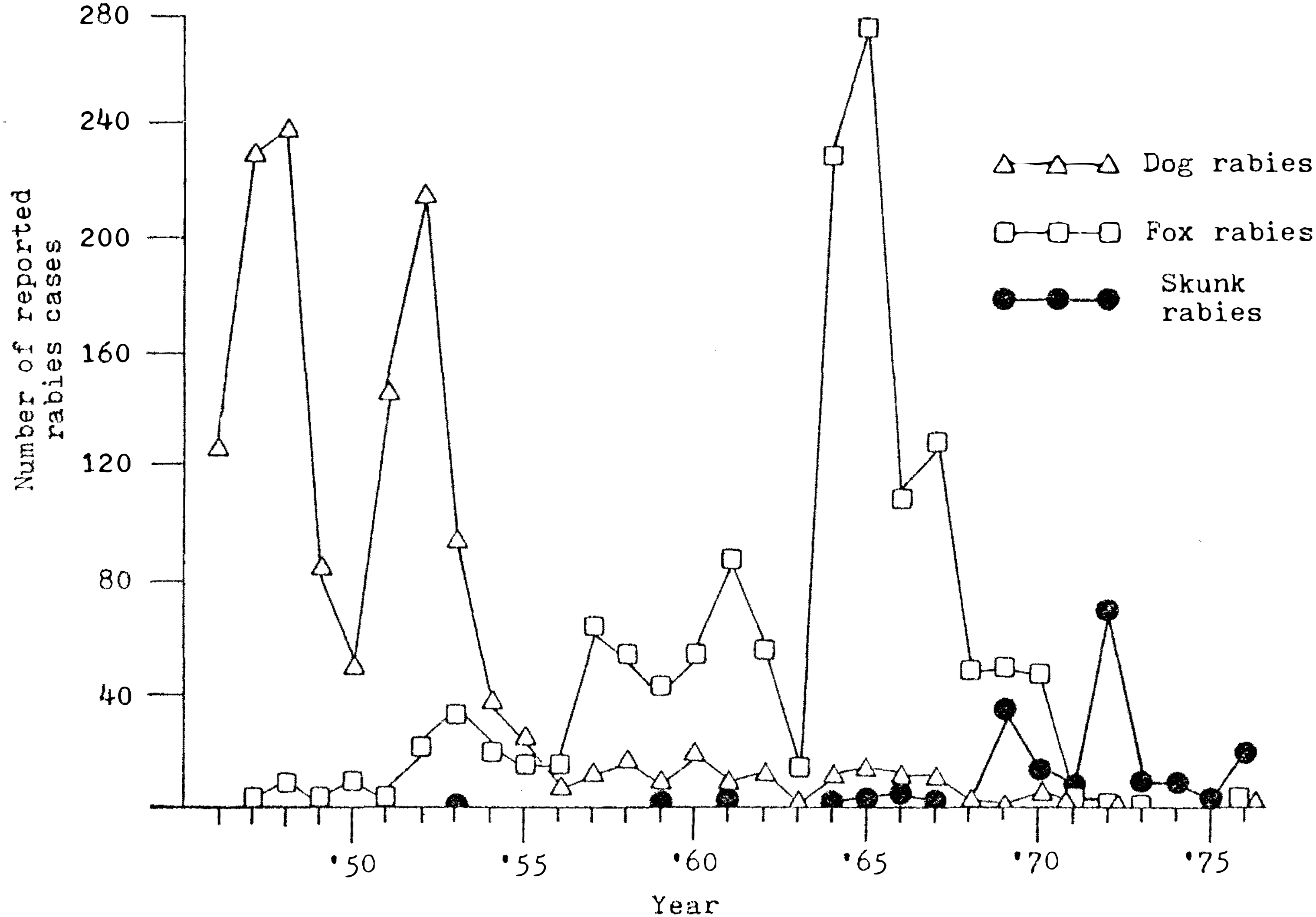


Fig. 9. Incidence of reported rabies cases in the 30 county study region among three major animal categories, 1946-1976.

Table 11. Historical trend in the number of counties in the study region with reported rabies cases, 1946-1976.

Year	Major rabies host	Counties with data	Counties with reported rabies cases: Major host Number	Major host Percent	All species Number	All species Percent
1946	Dog	19	15	79	16	84
1947	Dog	19	18	95	18	95
1948	Dog	19	16	84	16	84
1949	Dog	19	16	84	16	84
1950	Dog	19	8	42	11	58
1951	Dog	22	14	63	14	63
1952	Dog	30	14	47	17	57
1953	Dog	30	13	43	14	47
1954	Dog	30	13	43	17	57
1955	Dog	30	10	33	13	43
1956	Fox	30	6	20	11	37
1957	Fox	30	7	23	10	38
1958	Fox	30	12	40	15	50
1959	Fox	30	8	27	12	40
1960	Fox	30	8	27	11	37
1961	Fox	30	8	27	8	27
1962	Fox	30	10	33	11	37
1963	Fox	30	3	10	7	23
1964	Fox	30	11	37	13	43
1965	Fox	30	19	63	19	63
1966	Fox	30	15	50	18	60
1967	Fox	30	15	50	18	60
1968	Fox	30	8	27	11	37
1969	Fox	30	5	17	7	23
1970	Fox	30	5	17	7	23
1971	Skunk	30	5	17	7	23
1972	Skunk	30	10	33	14	47
1973	Skunk	30	4	13	4	13
1974	Skunk	30	6	20	7	23
1975	Skunk	30	2	7	3	10
1976	Skunk	30	4	13	8	27

reporting rabid animals which occurred as the major rabies host species changed was also associated with changes in the particular counties which reported rabies cases. From 1946 through 1955 at least one case of dog rabies was reported in 87 percent (26/30) of the counties in the study region. The four North Carolina counties of Jackson, Madison, Mitchell, and Yancy were completely free of reported dog rabies cases from 1952 through 1955. The 1957-1962 period was arbitrarily chosen to represent the enzootic fox rabies condition in the region. During these six years reported cases of animal rabies occurred almost exclusively in the northern half of the region (Fig. 10). During the six years in which the skunk was the major rabies host, 1971-1976, reported animal rabies cases occurred in a pattern which was approximately linear from the northeast to the southwest and conformed, to some extent, to the major valley section of the region (Fig. 11). This pattern was most evident during 1974 and 1976.

Another aspect of the spatial pattern of reported rabies cases is the recurrence pattern, the degree of similarity between counties reporting rabid animals in different years. This similarity may be expressed by the point correlation coefficient which measures the degree of association. There was a difference in the pattern of rabies recurrence between the period selected to represent the enzootic fox rabies condition, 1957-1962, and the period during which the skunk

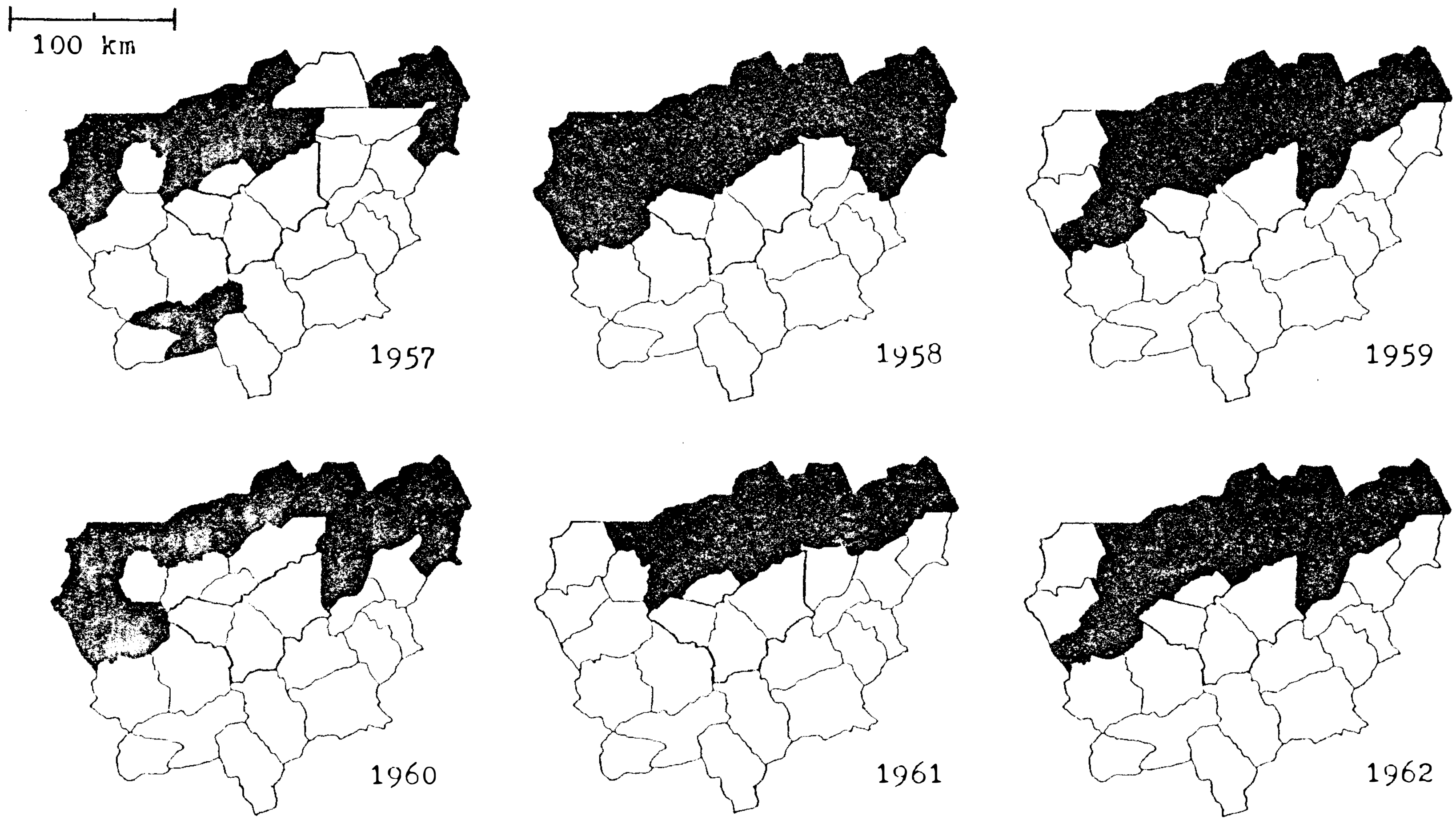


Fig. 10. Geographical pattern of rabies during the period characterized by enzootic fox rabies, 1957-1962. Maps show in black those counties in the 30 county study region which reported a rabies case or cases (all species) during the year indicated.

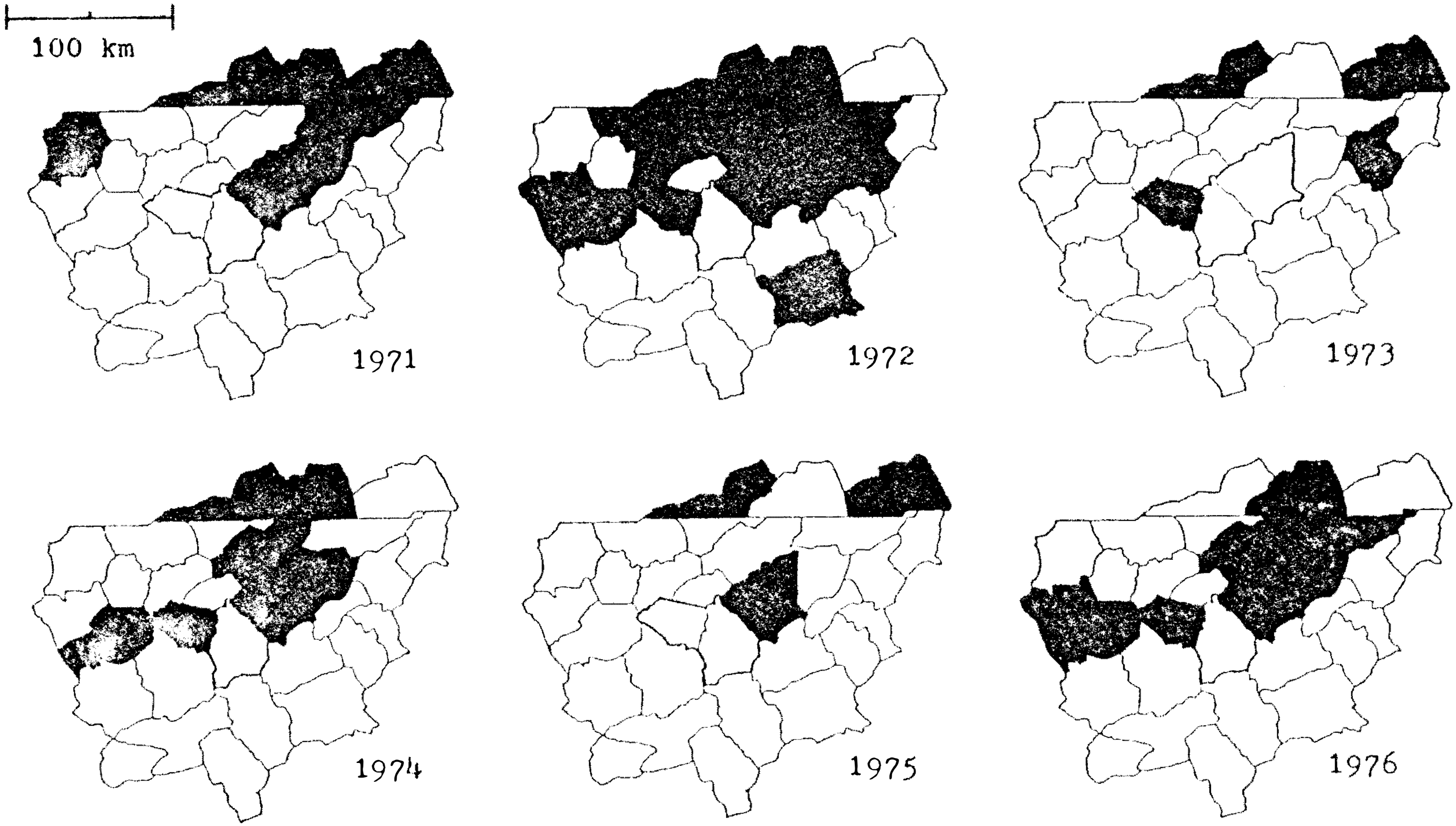


Fig. 11. Geographical pattern of rabies during the period characterized by enzootic skunk rabies, 1971-1976. Maps show in black those counties in the 30 county study region which reported a rabies case or cases (all species) during the year indicated.

was the major rabies host (Table 12). During the period of enzootic fox rabies, reported rabies cases recurred in many of the same counties after one year, had slightly less similarity after two years, and again showed a similar pattern after three and four years. While the number of reported cases fluctuated, rabid animals seemed to reappear year after year in, for the most part, similar counties during the period characterized by enzootic fox rabies.

During the 1971-1976 period rabid animals seemed to recur in similar patterns after two and four years, but showed less similarity after one and three years. This sequence was not evident for the pattern based on the location of rabid animals in 1971, but as the period of enzootic skunk rabies progressed the recurrence of rabid animals in the same geographical pattern after two and four years became more pronounced.

While biases in the reporting of rabies cases must always be considered, some generalizations seem evident. A persistent fox rabies problem did not arise in all the counties which had experienced a problem with rabid dogs. Specifically, most of the counties in the southern part of the region ceased to have a significant rabies problem of any kind after the decline in rabies among dogs. Furthermore, some of the counties with numerous cases of fox rabies did not develop a problem with rabid skunks during the 1970's. Specifically, rabid skunks have not become a significant problem in some of

Table 12. The recurrence pattern for reported rabies cases (all species) among the 30 counties of the study region during a six-year period of enzootic fox rabies, 1957-1962, and a six-year period of enzootic skunk rabies, 1971-1976.

Enzootic fox rabies

	Point correlation coefficient[a]				
	1958 (15)	1959 (12)	1960 (11)	1961 (8)	1962 (11)
1957 (10)	+0.57	+0.29	+0.49	+0.53	+0.34
1958		+0.68	+0.62	+0.60	+0.63
1959			+0.51	+0.44	+0.93
1960				+0.48	+0.57
1961					+0.79

	Average recurrence coefficient for analogous years
+4 years	+0.58
+3 years	+0.67
+2 years	+0.48
+1 year	+0.61

Enzootic skunk rabies

	Point correlation coefficient				
	1972 (14)	1973 (4)	1974 (7)	1975 (3)	1976 (8)
1971 (7)	+0.27	+0.25	+0.44	+0.60	+0.38
1972		+0.22	+0.59	+0.13	+0.64
1973			+0.25	+0.52	+0.29
1974				+0.34	+0.74
1975					+0.05

	Average recurrence coefficient for analogous years
+4 years	+0.62
+3 years	+0.29
+2 years	+0.52
+1 year	+0.23

[a]The degree of association is expressed by the point correlation coefficient which ranges from +1 for totally identical patterns to -1 for total dissimilarity. Numbers in parentheses are the counties reporting rabies cases during the year.

the northeastern and northwestern counties of the region.

It is evident from the preceding considerations that the counties in the north-central part of the region have experienced the most persistent problem with reported animal rabies cases. Rabies incidence data for all 30 counties are available for the 25 year period from 1952 through 1976. The persistence of reported rabies cases among the several animal categories can be expressed by the number of years in which at least one rabies case was reported in the county (Table 13). Considering the study region as a whole, some rabies cases were reported in each year, but rabid foxes occurred in 23 years (92 percent), rabid dogs in 22 years (88 percent), and rabid skunks in only 15 years (60 percent) of the 25-year period.

There is no precise, quantitative definition to use in determining which counties might constitute macrofoci of rabies infected animals. If a macrofocus is defined as a county with reported rabies cases in every year under consideration, then no rabies macrofoci existed within the study region. However, rabid animals often occur sporadically even in areas with a persistent, long-term rabies problem. Therefore, the author postulated that those counties with reported rabies cases in more than 50 percent of the years that the disease occurred in a given animal category within the study region as a whole were centers of rabies infection for that particular animal category. Based on this arbitrary

Table 13. Persistence of rabies among the various animal categories in the 30 county study region, 1952-1976.[a]

County	Dog	Cat	Cow	Fox	Skunk	Bat	Other	Total[b]
Anderson, Tenn.	25/ 7	2/2	9/ 4	48/ 9	1/1	1/1	3/3	89/14
Blount, Tenn.	51/ 3	5/2	1/ 1	1/ 1	-	-	-	58/ 4
Buncombe, N.C.	1/ 1	-	-	-	-	2/1	-	3/ 3
Campbell, Tenn.	18/ 6	5/4	10/ 6	15/ 8	-	-	3/3	51/12
Carter, Tenn.	4/ 3	3/3	5/ 2	16/ 4	13/2	-	1/1	42/ 6
Claiborne, Tenn.	13/ 6	3/2	20/ 8	59/11	4/3	-	1/1	100/15
Cocke, Tenn.	5/ 4	-	7/ 2	42/ 4	-	-	-	54/ 5
Graham, N.C.	4/ 2	-	-	-	-	-	-	4/ 2
Grainger, Tenn	21/ 8	10/7	24/ 7	55/11	4/2	-	-	115/14
Greene, Tenn.	7/ 4	7/2	29/ 5	147/ 5	66/6	1/1	5/3	262/12
Hamblen, Tenn.	4/ 4	2/2	9/ 5	67/ 6	2/1	-	-	84/11
Hancock, Tenn.	7/ 6	3/3	13/ 8	48/12	1/1	-	2/2	74/15
Hawkins, Tenn.	19/12	8/6	21/ 9	70/11	6/2	-	-	124/17
Haywood, N.C.	13/ 2	1/1	1/ 1	-	-	2/1	1/1	18/ 3
Jackson, N.C.	-	-	-	-	-	-	-	-
Jefferson, Tenn.	7/ 4	-	2/ 2	17/ 4	9/2	-	-	35/ 9
Johnson, Tenn.	-	1/1	9/ 4	11/ 6	-	-	-	21/ 7
Knox, Tenn.	222/ 9	10/4	15/ 6	7/ 4	3/2	8/7	1/1	266/17
Lee, Va.	20/13	9/4	52/ 8	122/18	19/9	1/1	6/3	229/23
Madison, N.C.	-	-	-	-	-	1/1	-	1/ 1
Mitchell, N.C.	-	-	-	-	-	-	-	-
Scott, Va.	22/13	20/9	44/14	170/17	8/7	-	4/4	268/21
Sevier, Tenn.	9/ 2	4/3	-	4/ 2	-	-	-	17/ 5
Sullivan, Tenn.	9/ 7	6/3	22/ 7	145/12	23/4	3/2	3/2	211/17
Swain, N.C.	5/ 3	1/1	-	-	-	-	-	6/ 4

Table 13. continued.

County	Dog	Cat	Cow	Fox	Skunk	Bat	Other	Total[b]
Unicoi, Tenn.	-	-	-	1/ 1	1/1	-	1/1	3/ 3
Union, Tenn.	5/ 5	-	6/ 4	16/ 9	2/2	-	1/1	30/12
Washington, Tenn.	4/ 3	3/2	8/ 3	36/ 5	16/5	2/2	2/2	71/13
Washington, Va.	17/10	17/8	52/16	288/16	3/3	1/1	8/5	386/20
Yancy, N.C.	-	-	-	-	-	-	-	-
Study region								
Total rabies cases	512	120	359	1,385	181	22	43	2,622
Number of years (of 25) with reported cases	22	19	21	23	15	11	16	25

[a]Data show total number of reported cases/number of years (of 25) in which a case or cases were reported.

[b]Since counties frequently reported rabies cases in several animal categories, the total number of years with rabies cases does not equal the sum of the years with rabies cases among the different animal categories.

definition, the centers of rabies among dogs were Hawkins, Scott, and Lee counties (Fig. 12). The centers of rabies among foxes were Hancock, Lee, Scott, Sullivan, and Washington (Va.) counties. The only center for rabies among skunks was Lee County. There was a distinct persistence of reported bat rabies cases in Knox County, but this may have reflected the fact that the county has the largest human population in the study region.

Considering the three major terrestrial carnivores, there were six different counties which appeared to be centers, or foci, of reported rabies cases. These six counties form a continuous area in the northern part of the study region. Lee County was unique in that it fulfilled the criterion as a center of reported rabies cases among dogs, foxes, and skunks. This county reported some animal rabies cases in 23 of the 25 years considered, the highest number of years for any county in the study region. Scott County, immediately east of Lee County, was considered to be a center for both dog and fox rabies, and it was second to Lee County in the number of years in which rabid skunks were reported. In a relative sense, the reported rabies cases within the study region appeared to be highly concentrated in the north-central part of the region, particularly Lee County.

The apparent persistence of reported rabies cases in the north-central counties of the region may be considered

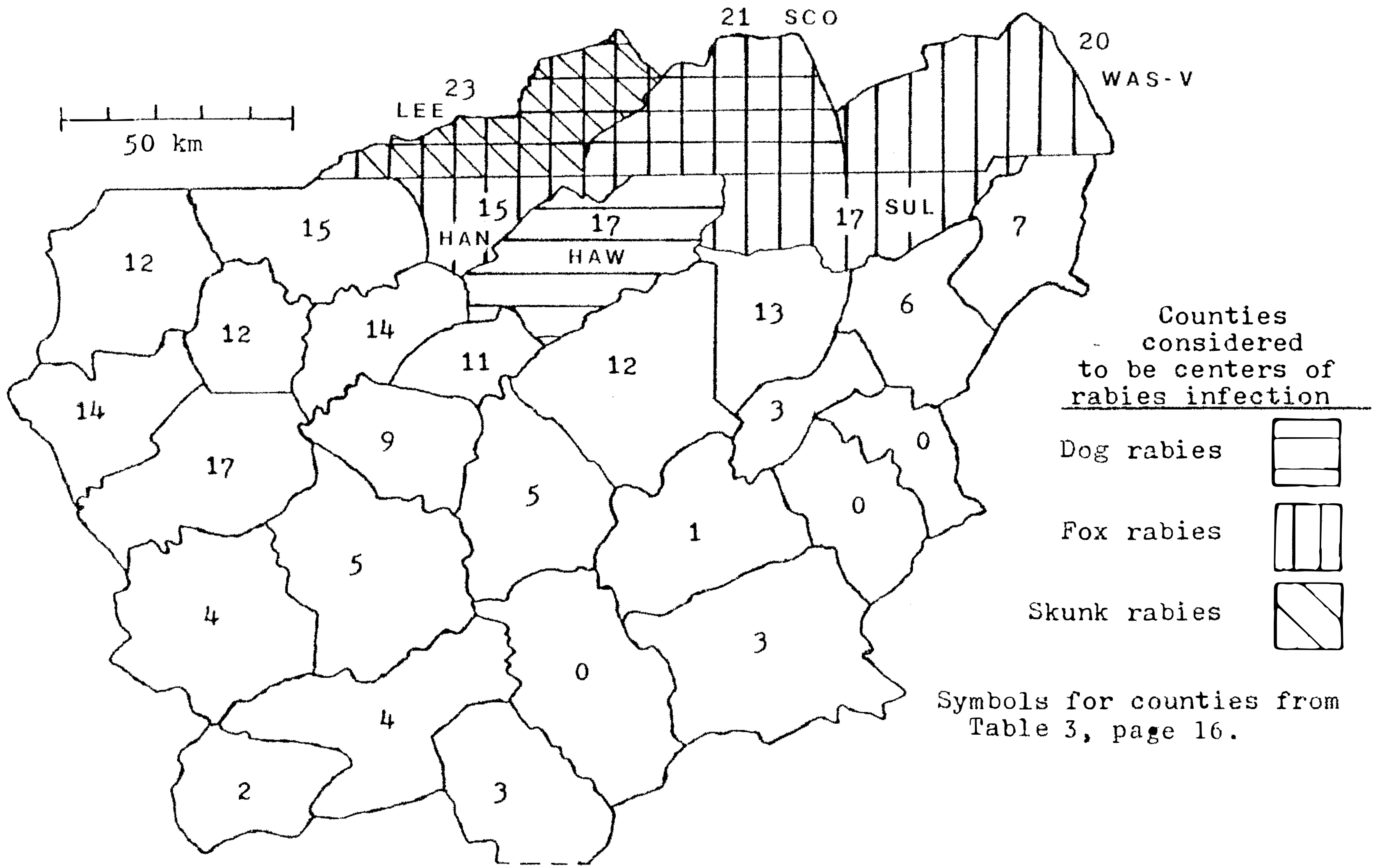


Fig. 12. Counties considered to be centers of rabies infection for the three major rabies hosts. Numbers represent the years during which a rabies case or cases (all species) were reported in the county, 1952-1976.

in relation to the emergence of rabies in skunks. Lee County had a persistent dog rabies problem and the most persistent fox rabies problem of any county in the study region. The first two reported cases of skunk rabies occurred as single cases during 1953 and 1959. Both of these rabid skunks were found in Lee County. The first year with multiple reported skunk rabies cases was 1961, and these cases occurred as single rabid skunks in Lee County and the adjacent county to the south, Hancock (Fig. 13). From this two county area the initial cases of reported skunk rabies appeared to radiate eastward into the other two Virginia counties of the study region and southward into some counties of northeastern Tennessee. No rabid skunks have been reported from the eight North Carolina counties of the study region.

The progressive spread of reported skunk rabies cases did not appear to be strongly influenced by the large fox rabies epizootic of the mid-1960's. This outbreak appeared initially in the center of the study region during 1964 (Fig. 14) and spread to the northeast. During the period from 1965 through 1967 initial skunk rabies cases occurred in counties north and west of the counties with the largest number of reported fox rabies cases. While the fox rabies outbreak appeared to progress northeasterly, the initial occurrence of reported skunk rabies cases within the counties of the study region progressed southwesterly during the 1965-1967 period.

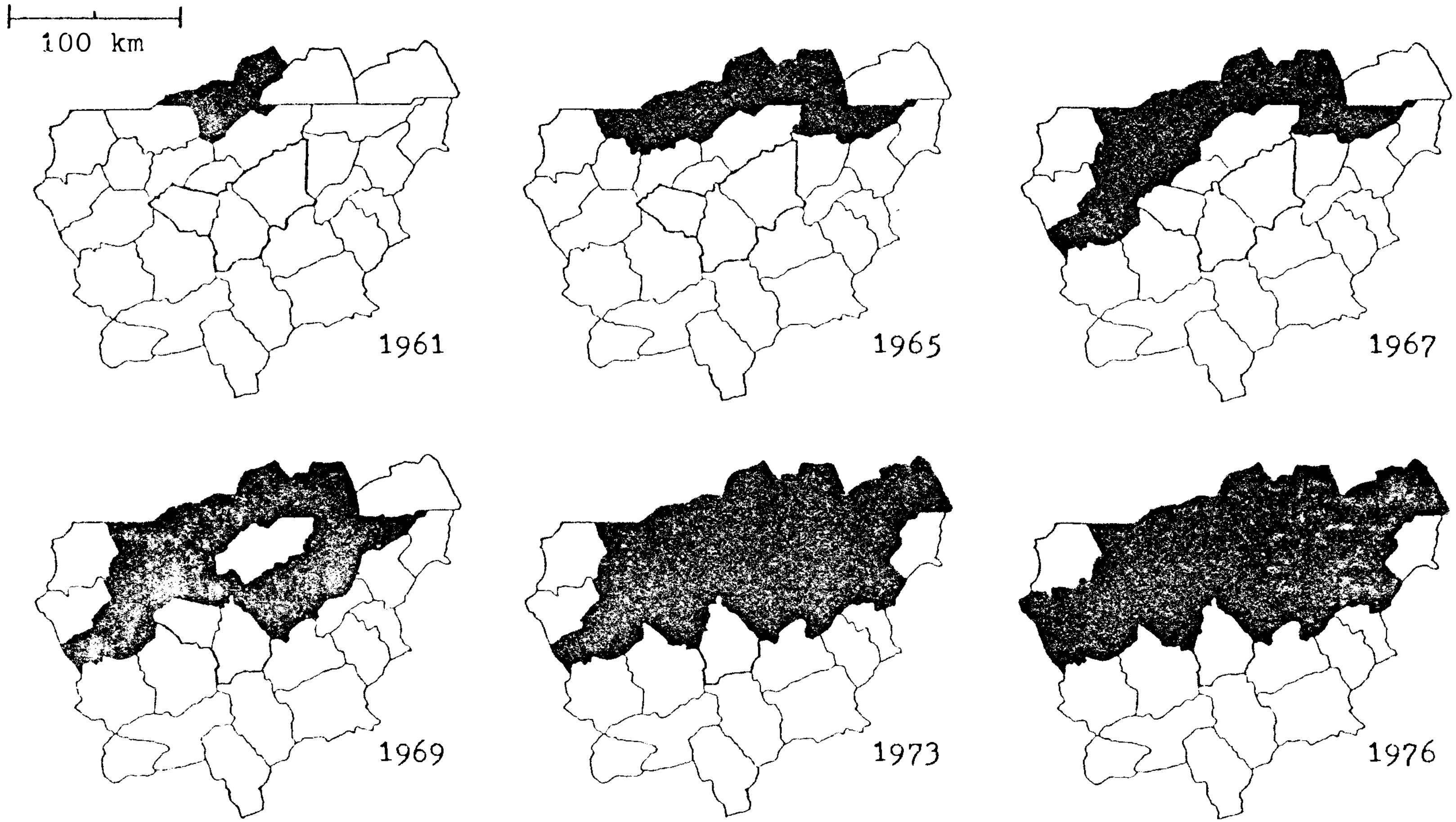


Fig. 13. Progression of reported skunk rabies cases through the study region. Maps show in black those counties which reported the initial case(s) of skunk rabies during or prior to the year indicated.

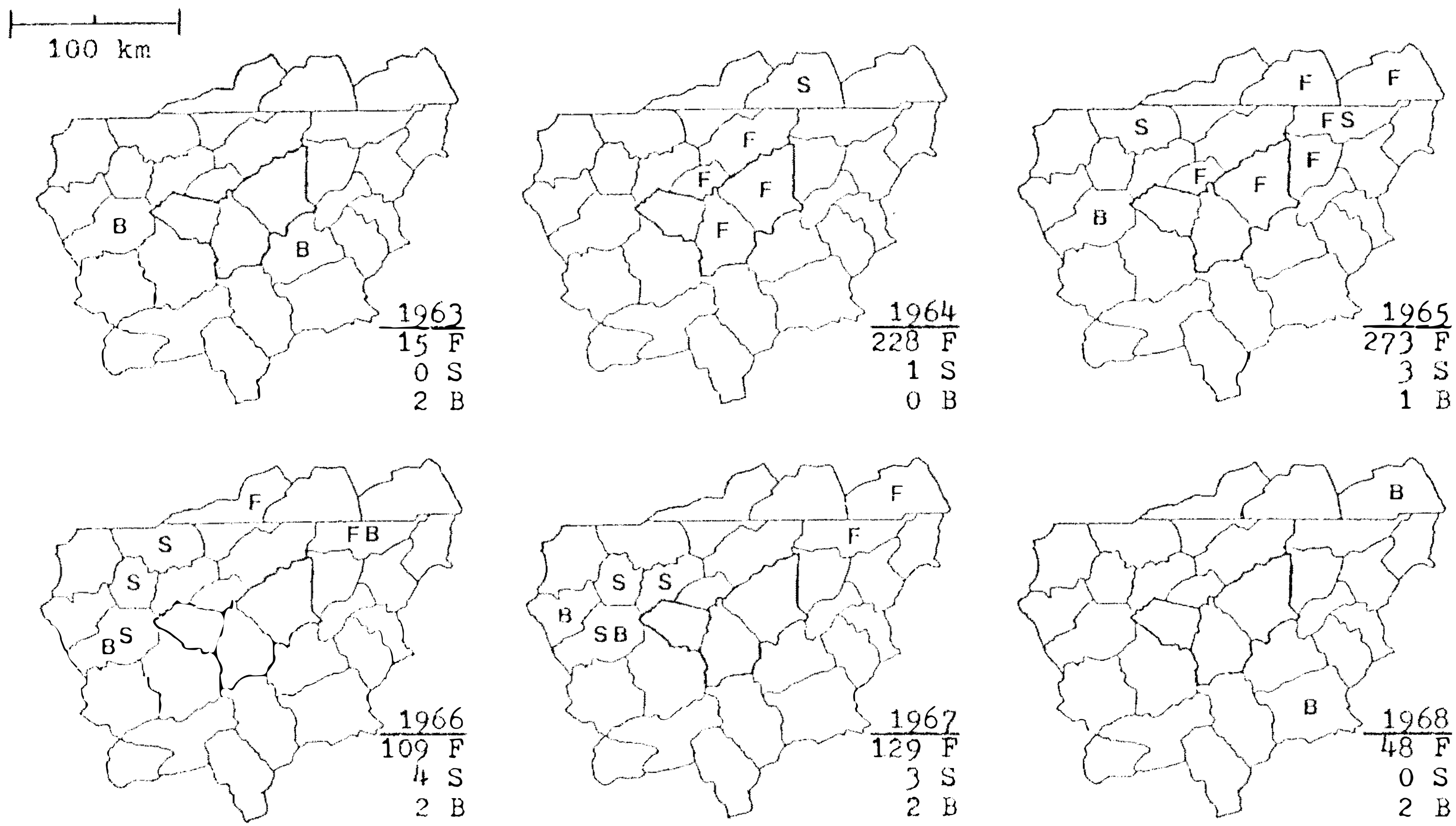


Fig. 14. The fox rabies epizootic in the study region in relation to the occurrence of reported rabies cases in bats and skunks. Maps show those counties with 20 or more reported fox rabies cases (F), skunk rabies case(s) (S), and bat rabies case(s) (B) for the year indicated.

There are several interesting aspects associated with the major fox rabies outbreak of 1964-1967. The outbreak was most apparent in Greene and Cocke counties during 1964. Neither of these counties reported any rabies cases during the period of enzootic fox rabies (Fig. 10, p. 61). Greene County reported only one rabies case, a dog in 1953, during the 14 years prior to the 1964 outbreak, but in 1964 there were 101 reported cases of fox rabies in the county. During 1963 there were only 15 rabid foxes reported in the study region, the lowest number since 1951. It is interesting to note that during 1963 the first cases of bat rabies were reported in the study region with one case in Madison County and one case in Knox County. Madison County is south of and adjacent to both Greene and Cocke counties. The boundary of Madison County with the two Tennessee counties is an area of mountainous forest. There are no available data to suggest a link between the initial occurrence of reported bat rabies cases and the large fox rabies epizootic which began the following year.

II. RABIES IN THE STUDY AREA

From 1946 through 1976 there were 407 reported rabies cases among 10 animal categories in the three county study area (Table 14). Of this total 46 cases (11 percent) occurred in Jefferson County, 66 cases (16 percent) occurred in Cocke County, and 295 cases (72 percent) were reported from Greene

Table 14. Total number of laboratory confirmed rabies cases among the major animal categories in the three county study area, 1946-1976

Animal category	Number of reported rabies cases	Percentage of total
Fox	210	51.6
Skunk	75	18.4
Dog	52	12.8
Cow	51	12.5
Cat	13	3.2
Horse	2	0.2
Swine	1	0.2
Muskrat	1	0.2
Bobcat	1	0.2
Bat	1	0.2
Total	407	

County. The 101 rabid foxes reported in Greene County during 1964 represented almost 25 percent of all the rabid animals reported in the study area during the 31-year period. The available data on the history of rabies in each of the three counties are presented in Appendix H.

In the study area the major rabies host changed in a pattern similar to that observed in the study region. The study area, however, experienced several years without any reported rabies cases. These rabies-free years seemed to separate the years characterized by reported rabies cases in one or two of the animal categories. The years with reported rabies may be grouped into four periods which can be designated by the major rabies host or hosts (Table 15). This procedure shows that the study area had a dog rabies problem, then a fox rabies problem, and was experiencing rabies cases predominantly among skunks during the study. These changes in the major rabies host are shown graphically in Fig. 15.

While the period characterized by fox rabies is considered to last from 1964 to 1967, it is apparent that each county experienced a single uninterrupted outbreak which lasted, at most, 16 months (Fig. 16). The outbreak of fox rabies began during January 1964 in Greene County which had been free of reported fox rabies cases since 1948 and free of any reported rabies cases since a single rabid dog during 1953. The data indicate that the fox rabies epizootic in Greene County developed gradually over the 10 months from

Table 15. The rabies history of the three county study area divided into periods of unequal duration in which reported rabies cases occurred predominantly in one or two animal categories.[a]

Year	Incidence of reported rabies during period: Dog	Cow	Fox	Skunk	Other	Total	Designation of period
1946 1947 1948 1949 1950	33/38*	13/16*	4/5*	0/*	6/10*	56/69*	Dog rabies
1951	Rabies free (0/2*)						
1952 1953 1954 1955[b] 1956	6/19*	0/1*	4/6*	0/1*	0/11*	10/38*	Dog/Fox rabies
1957 1958 1959 1960 1961 1962 1963	Rabies free (0/141*[c])						
1964 1965 1966 1967	12/138	34/86	198/313	0/2	10/203	254/742	Fox rabies
1968	Rabies free (0/55)						
1969 1970 1971 1972 1973 1974 1975 1976	1/205	4/28	4/98	75/87	3/312	87/730	Skunk rabies
Total	52/439*	51/134*	210/423*	75/92*	19/583*	407/1,777*[c]	

[a]Data show number of rabies cases/number of animals examined.

[b]Rabies free year within designated period.

[c]Includes the examination of 101 unspecified animals.

*Data not available or incomplete.

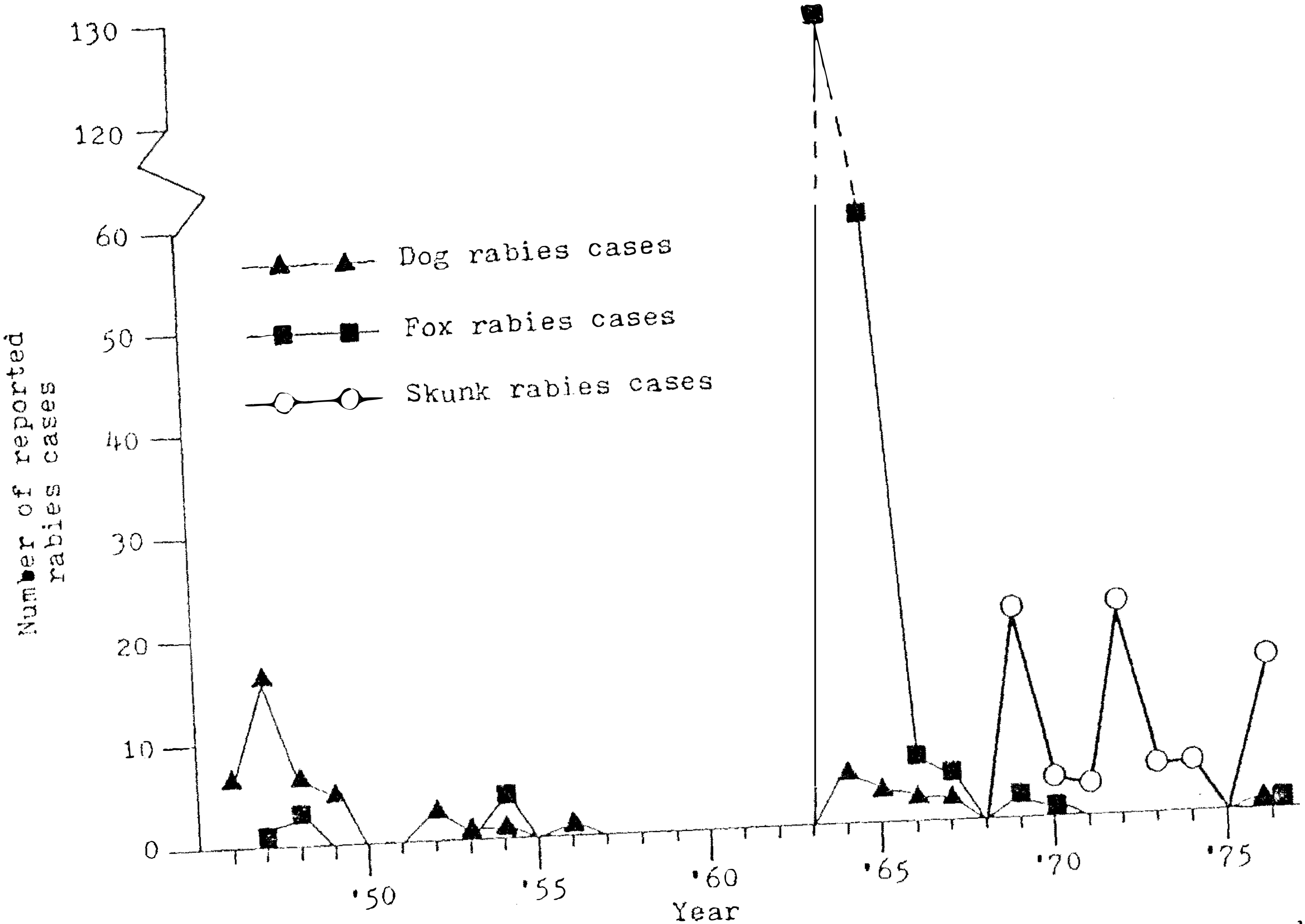
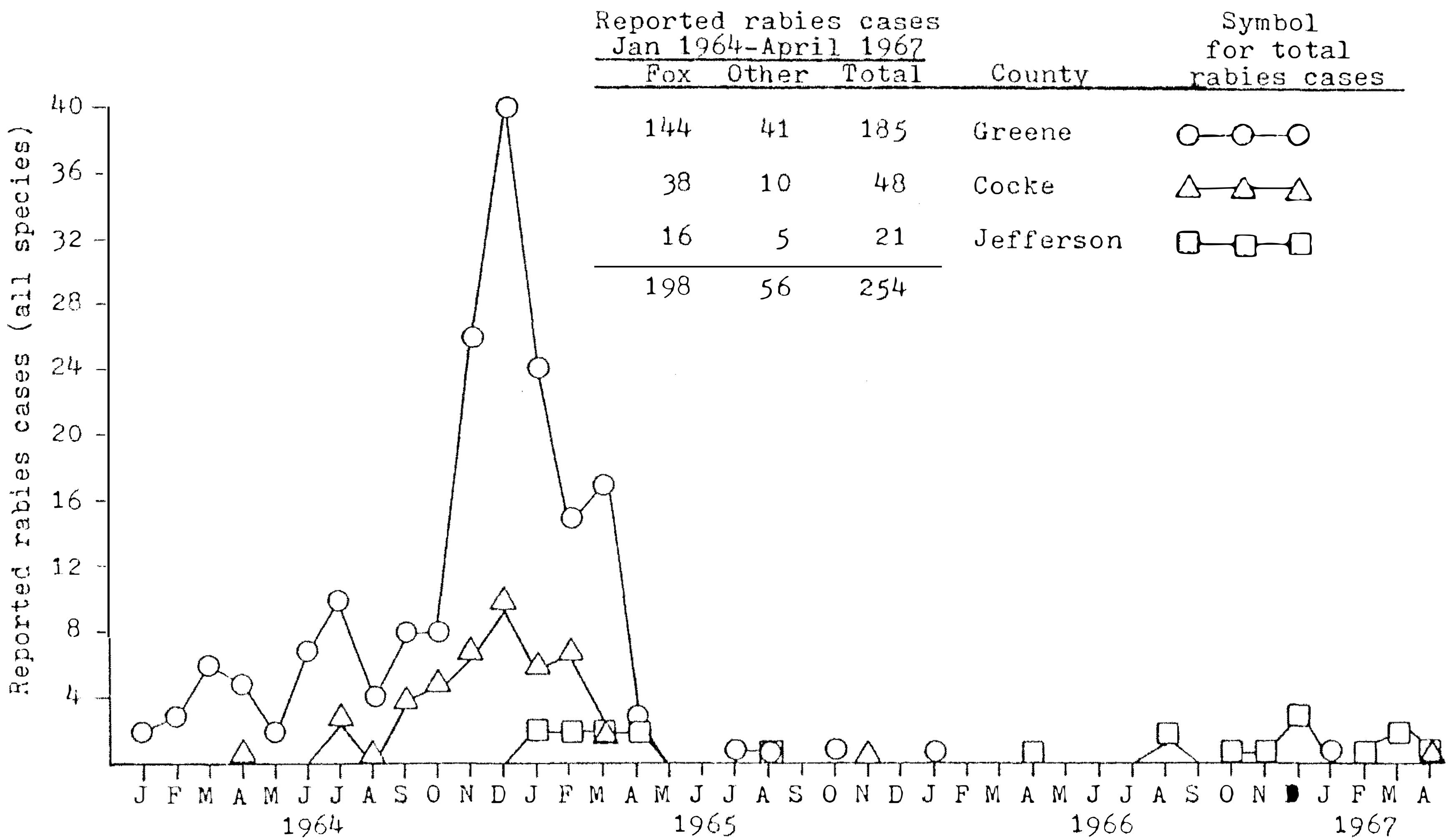


Fig. 15. Incidence of reported rabies in the three county study area among the three major animal categories, 1946-1976.



Reported rabies cases Jan 1964-April 1967 Fox	Other	Total	County	Symbol for total rabies cases
144	41	185	Greene	O—O—O
38	10	48	Cocke	△—△—△
16	5	21	Jefferson	□—□—□
198	56	254		

Fig. 16. Monthly incidence of reported rabies cases (all species) in the three counties of the study area during the period characterized by high levels of fox rabies, January, 1964-April, 1967.

January to October 1964, erupted during November, lasted for five months with a peak in December, and quickly subsided after March 1965. The duration and extent of the fox rabies outbreaks in the other two counties appeared to be inversely related to their distance from Greene County. Beginning in July 1964 Cocke County reported rabid foxes for nine continuous months with a peak monthly incidence during December. Jefferson County, which is not adjacent to Greene County but does adjoin Cocke County, reported rabid foxes initially in January 1965 and experienced reported fox rabies cases for only four continuous months. The fox rabies outbreaks in these three counties began at staggered intervals, but reported fox rabies cases appeared to terminate rather uniformly in the study area during March and April of 1965.

While sporadic cases of rabies among foxes and other animals occurred in the study area after April 1965, the disease did not appear to become enzootic in the area. Both Greene and Jefferson counties continued to report sporadic rabies cases among foxes and other animals until the spring of 1967. The study area was free of reported rabies cases from May 1967 until February 1969, a period of 21 months without any reported rabies cases.

Early in 1969 the first reported cases of skunk rabies occurred in the study area. While the upsurge of fox rabies within the three counties occurred over a relatively short period of time, the initial appearance of reported skunk rabies cases has occurred in only two of the counties, and these cases were separated by approximately four years. In Greene County rabies was reported in 143 foxes and 40 other animals during the 1964-1965 period, but rabid skunks were first reported during 1969. Jefferson County had an upsurge of rabid foxes during the 1965-1967 period (16 cases), and the county initially reported rabid skunks during 1973. Cocke County also had a small outbreak of fox rabies during 1964-1965 (37 cases), but there have been no reported cases of skunk rabies in the county. In fact, Cocke County remained free of any reported rabies cases from April 1967 through 1976.

During 1969 there were 21 rabid skunks reported in Greene County. Seven additional cases of skunk rabies were reported during the 1970-1971 period. The first and only rabid bat reported in the study area occurred during 1971 in Greene County. Data are not available on the location of these and other rabid animals within Greene County.

The present study which began during 1973 attempted to gather, retrospectively, detailed information on the rabies cases which occurred in 1972. This information included data on animals submitted for rabies examination by month by animal category. The available data for the five years of 1972-1976 are presented in Appendix I.

During 1972, 150 animals from the study area were examined for rabies and 24 (16 percent) were found to be rabid. These 24 animals included 22 skunks and two cows (Table 16). Considering that the human population of the Jefferson-Cocke County area was similar to that of Greene County, the per capita submission rate of the latter area (109 animals examined) was approximately 2.5 times greater than the two county unit (41 animals examined) which had been free of reported rabies since early 1967. Locations were obtained for 18 of these 24 cases (Fig. 17). Based on the general address given with the other six cases, there is reason to believe that some of these rabid skunks occurred in the same general part of Greene County as the cases with documented locations. The 18 rabid animals which were located were not randomly distributed among the 48 trap areas ($P < .01$). One rabid cow and 16 rabid skunks were clustered in the eastern part of Greene County.

During 1973 there were five reported rabies cases in the study area (Table 17). These cases were all among striped skunks in Jefferson County and constituted the first reported incidence of the disease in skunks of that county. While Greene County was free of reported rabies cases during 1973, the 43 animals submitted from the county exceeded the combined number of submissions from the Jefferson-Cocke County area, 33 animals.

During 1974 there were again five reported rabies cases among striped skunks in the study area (Table 17).

Table 16. Reported rabies cases in the study area, 1972.

Designated number	Date	Species	Location	
			County	Trap area
72-1	3 Jan.	Striped skunk	Greene	46
72-2	3 Feb.	Skunk[a]	Greene	46
72-3	29 Feb.	Striped skunk	Greene	40
72-4	7 March	Striped skunk	Greene	39
72-5	7 March	Striped skunk	Greene	46
72-6	10 March	Striped skunk	Greene	44
72-7	13 March	Skunk[a]	Greene	*
72-8	13 March	Striped skunk	Greene	40
72-9	15 March	Striped skunk	Greene	42
72-10	20 March	Striped skunk	Greene	39
72-11	21 March	Striped skunk	Greene	34
72-12	22 March	Striped skunk	Greene	46
72-13	28 March	Striped skunk	Greene	44
72-14	28 March	Striped skunk	Greene	34
72-15	28 March	Striped skunk	Greene	39
72-16	7 April	Striped skunk	Greene	34
72-17	13 April	Skunk[a]	Greene	*
72-18	26 April	Skunk[a]	Greene	*
72-19	9 May	Skunk[a]	Greene	*
72-20	16 May	Skunk[a]	Greene	*
72-21	14 June	Striped skunk	Greene	39
72-22	14 July	Skunk[a]	Greene	*
72-23	16 Aug.	Cow	Greene	43
72-24	13 Sept.	Cow	Jefferson	8

[a]Species of skunk not available.

*Data not available.

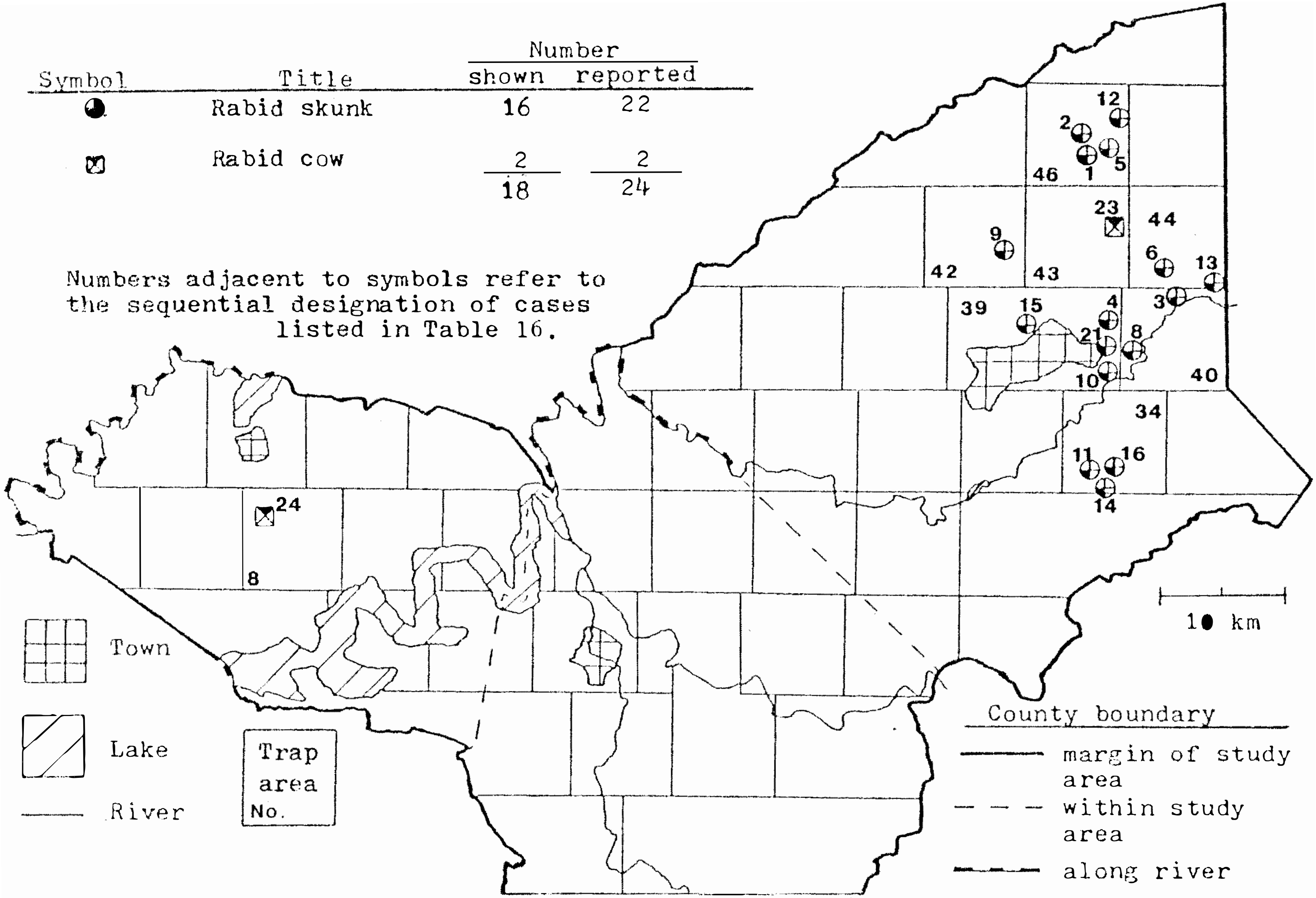


Fig. 17. Location of reported rabies cases in the study area (partial data), 1972.

Table 17. Reported rabies cases in the study area, 1973-1975.

Designated number	Date	Species	Location: County	Location: Trap area
1973				
73-1	3 March	Striped skunk	Jefferson	2
73-2	11 March	Striped skunk	Jefferson	1
73-3	11 March	Striped skunk	Jefferson	1
73-4	13 April	Striped skunk	Jefferson	2
73-5	30 Aug.	Striped skunk	Jefferson	1
1974				
74-1	1 April	Striped skunk	Jefferson	1
74-2	1 May	Striped skunk	Jefferson	1
74-3	* May	Striped skunk	Greene	45
74-4	11 June	Striped skunk	Jefferson	8
74-5	20 June	Striped skunk	Jefferson	4
1975				
75-1	25 April	Horse	Greene	45

*Data not available.

Four of these cases occurred in Jefferson County, and a single rabid skunk was reported from Greene County. There were 38 animals submitted from the Jefferson-Cocke County area, a sum equal to the number of animals submitted for examination in Greene County.

Only one rabid animal was reported in the study area during 1975. This rabid horse occurred in Greene County during April. The number of animals examined for rabies declined slightly from 1974, but the number of submissions from the Jefferson-Cocke County area (31 animals) was similar to the number examined from Greene County (32 animals).

The 11 reported rabies cases during the 1973-1975 period were not randomly distributed among the 48 trap areas ($P < .05$). Eight of the 10 rabid skunks were clustered in the northwestern part of Jefferson County (Fig. 18). The two reported rabies cases in northern Greene County were separated in time by 11 months, but were spaced less than 5 km apart. In Jefferson County all rabid skunks which were reported during March and April were located in either trap area 1 or 2. The two rabid skunks which occurred singularly in trap areas 4 and 8 were reported during June 1974.

During 1976 there was an upsurge in skunk rabies cases in the study area (Table 18). In Greene County 15 rabid striped skunks were reported. The single case of dog rabies may have resulted from exposure to a rabid skunk, since this dog was observed fighting with a skunk prior to

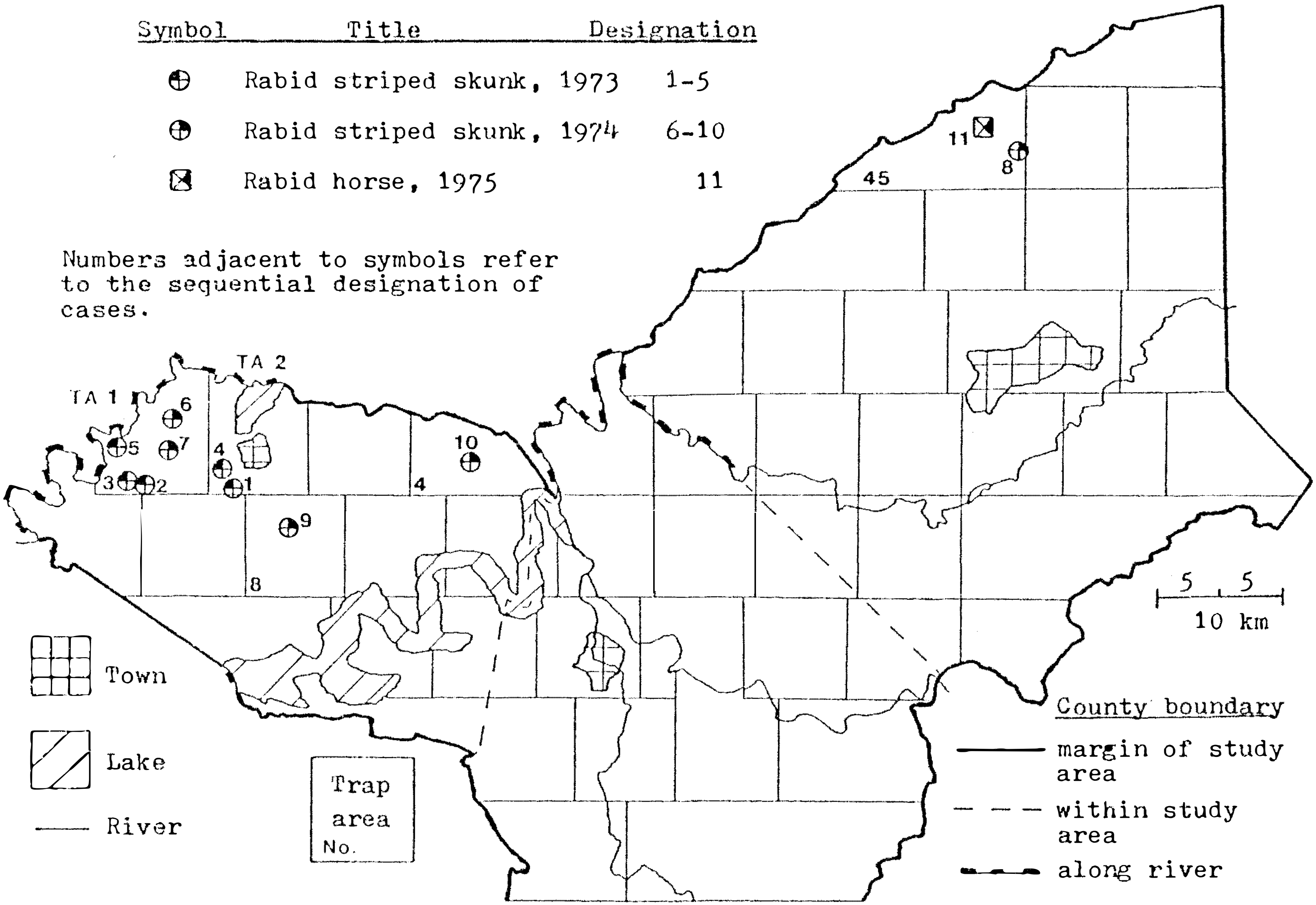


Fig. 18. Location of reported rabies cases in the study area, 1973-1975.

Table 18. Reported rabies cases in the study area, 1976.

Designated number	Date	Species	Location	
			County	Trap area
76-1	3 March	Striped skunk	Greene	47
76-2	3 March	Striped skunk	Greene	46
76-3	17 March	Striped skunk	Greene	44
76-4	14 April	Striped skunk	Greene	40
76-5	4 May	Striped skunk	Greene	44
76-6	7 June	Striped skunk	Greene	44
76-7	9 June	Striped skunk	Greene	44
76-8	24 June	Dog[a]	Greene	35
76-9	29 June[b]	Striped skunk	Greene	47
76-10	27 July	Striped skunk	Greene	40
76-11	27 Aug.	Striped skunk	Greene	43
76-12	20 Oct.	Striped skunk	Greene	43
76-13	10 Nov.	Striped skunk	Greene	46
76-14	23 Nov.	Striped skunk	Greene	34
76-15	23 Nov.[c]	Gray fox	Jefferson	3
76-16	1 Dec.	Striped skunk	Greene	43
76-17	8 Dec.	Striped skunk	Greene	43

[a]Dog had recently fought with a skunk.

[b]Officially reported in July.

[c]Officially reported in December.

developing rabies. A rabid gray fox was reported in Jefferson County during December. This case was the first rabid fox reported in the county since 1967 and the first rabid fox reported in the study area since 1970. The number of animals submitted for a rabies diagnosis in Greene County (75 submissions) was approximately three times larger than the number of animals examined from the Jefferson-Cocke County area (26 submissions). The number of submissions from Greene County during 1976 was approximately twice the number of animals examined from the county during either 1974 (38 submissions) or 1975 (32 submissions).

The reported rabies cases in the study area during 1976 were not randomly distributed among the 48 trap areas ($P < .01$). The rabid animals reported in Greene County during 1976 (Fig. 19) occurred in the eastern part of the county with a distribution remarkably similar to the pattern of reported rabies cases during 1972. The single rabid gray fox occurred in northern Jefferson County, and it was slightly east of the area where most of the rabid skunks were located during 1973 and 1974.

The data from the five-year period of 1972-1976 indicate that the skunk was the major animal among reported rabies cases. Ninety percent (47/52) of all reported rabies cases in the study area were among skunks. Of these 47 skunk rabies cases, the 40 documented cases were all among striped skunks. It is doubtful that any spotted skunks

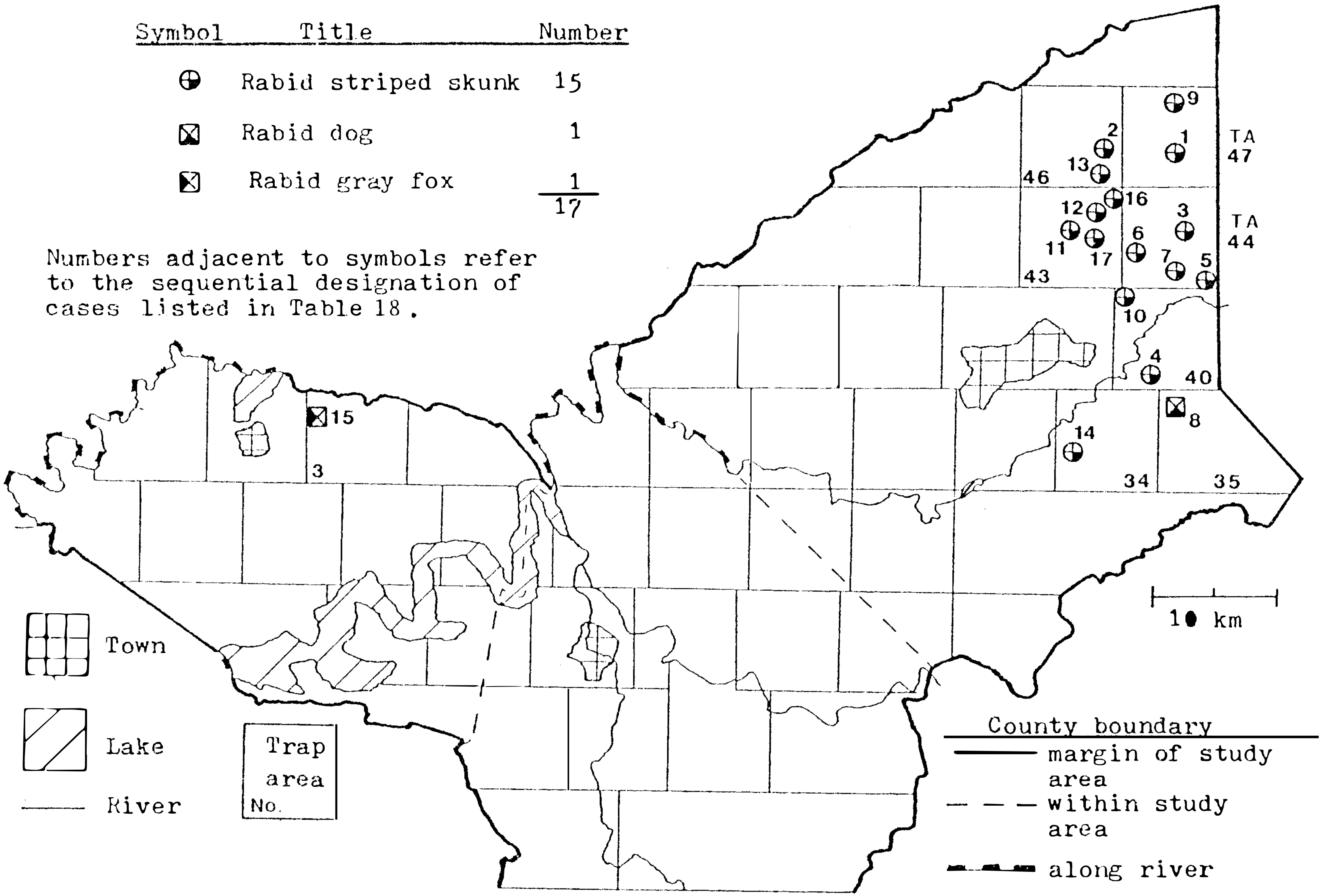
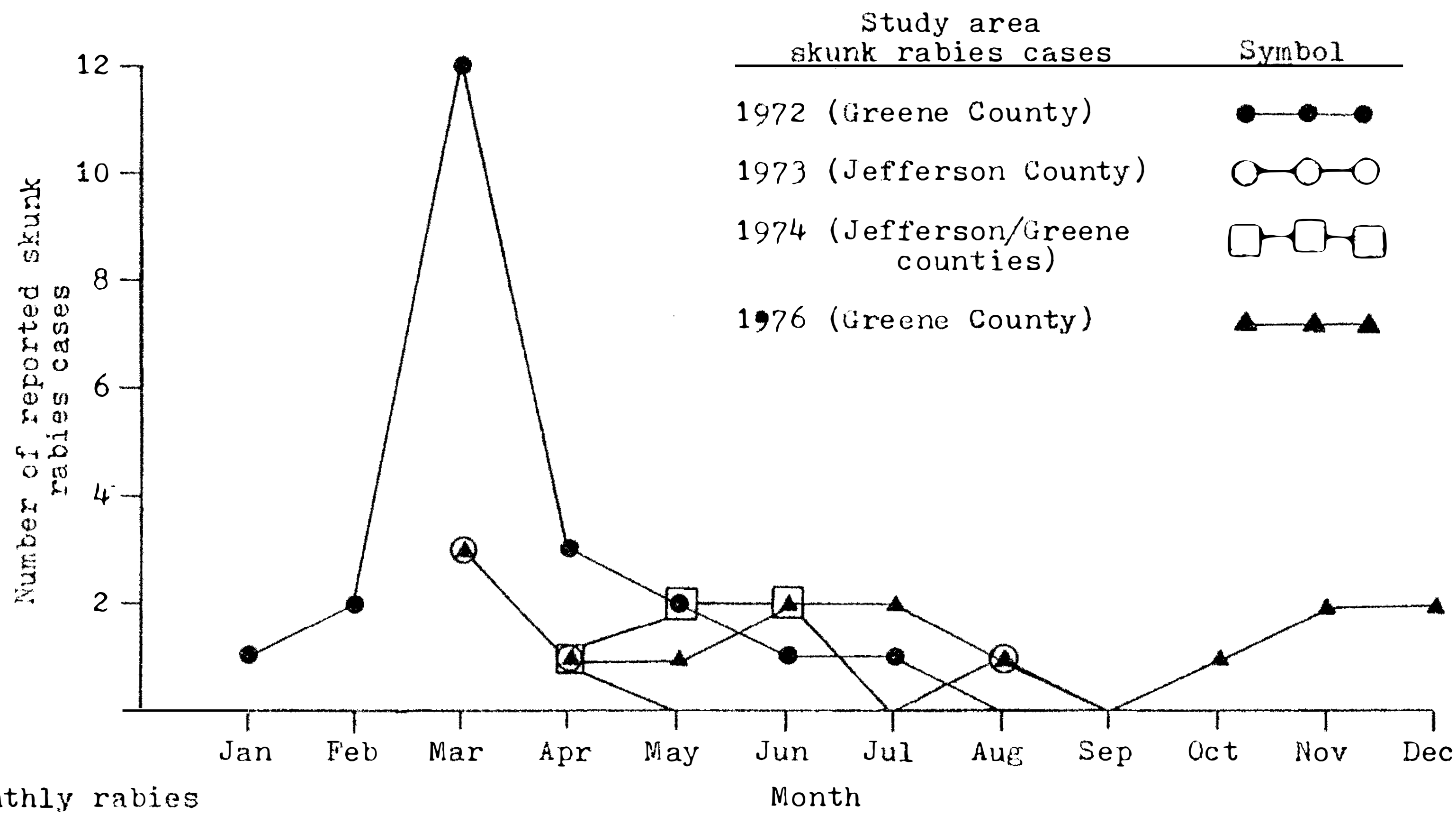


Fig. 19. Location of reported rabies cases in the study area, 1976.

(*Spilogale putorius*) were among the remaining seven cases.

The large percentage of skunks among the reported rabies cases was not a reflection of the submission data among the major animal categories. During the 1972-1976 period, 466 animals were submitted for a rabies diagnosis from the study area. This level of submissions would seem to indicate that the people of the area were concerned about the threat of rabies and utilized the diagnostic service of the state health department. During the five-year period, 123 dogs were examined and only one was found to be rabid, a positive diagnosis rate of only 0.8 percent. None of 120 cats examined were found to be rabid. Only one of the 68 foxes examined was found to be rabid, a positive diagnosis rate of 1.5 percent. The positive diagnosis rate among skunks was 87 percent (47/54). There was apparently a strong selection for rabid skunks prior to submission which was not evident among dogs, cats, or foxes.

Over the five-year period the monthly distribution of reported rabies cases differed from a random pattern in a highly significant manner ($P < .001$). Fifty-one percent (24/47) of all reported skunk rabies cases occurred during the months of March and April (Fig. 20). In three of the four years with reported skunk rabies cases, the initial case of the year occurred in either March or April, and after these initial cases, other rabid skunks usually continued into late spring and summer. Rabies cases among domestic animals



Monthly rabies incidence 1972-1976												
Skunk	1	2	18	6	5	5	3	2	0	1	2	2
Other	0	0	0	1	0	1	0	1	1	0	0	1

Fig. 20. Monthly incidence of reported rabies cases among skunks and other animals in the study area, 1972-1976. Data based on month of official report.

usually occurred after some or all of the rabid skunks had been reported with the exception of the rabid horse which occurred in late April of 1975. In three of the four years with rabid skunks, reported cases ceased after the summer months, but during 1976 there was a distinct resurgence of rabid skunks in the late fall and winter.

As seen in the considerations on the species composition of reported rabies cases, the monthly distribution of reported rabies cases did not appear to be a direct function of the number of animals examined (Table 19). While March did have the largest number of submissions, over 30 percent (18/59) of these animals were rabid, and the number of negative submissions during March was exceeded by the number during May, July, and August. Monthly submissions were highest from March through August, but the positive diagnosis rate for the July-August period was only 5.7 percent (6/105).

Interviews were conducted during the study in order to characterize the wild animals which were found to be clinically rabid and the circumstances surrounding their discovery and submission. This effort resulted in data on 39 rabid striped skunks and the single gray fox. The data available from the residents varied from case to case, and different areas of consideration, therefore, are based on groups of different size. Appendix J summarizes the findings of these interviews.

Rabid skunks were generally found very near the home

Table 19. Results of the state rabies diagnosis for animals of all species submitted from the study area, by month, 1972-1976.

Month	Animals submitted	Results of rabies diagnosis		
		Negative	Positive	
			Number	Percent
January	27	26	1	3.7
February	23	21	2	8.7
March	59	41	18	30.5
April	47	40	7	14.9
May	51	46	5	9.8
June	47	41	6	12.8
July	53	50	3	5.7
August	52	49	3	5.8
September	25	24	1	4.0
October	27	26	1	3.7
November	23	21	2	8.7
December	32	29	3	9.4
Total	466	414	52	11.2

of the resident who submitted the animal. The most common situation was the discovery of the skunk wandering in the yard adjacent to the house. A few skunks (5/39) were initially seen 50 to 100 m away from the home of the resident. The gray fox was discovered in a woodlot which was not near the home of the resident.

Most rabid animals were observed while still alive and during daylight hours. In seven of the 40 cases (18 percent), the animals were found dead or moribund. Three striped skunks had been killed after wandering toward or attacking dogs which were restricted to their kennel area. In case 76-1 the moribund skunk was carried into the yard of the resident in the mouth of the family dog. Among the 33 rabid animals which were alive at the time of discovery, 30 were first seen during daylight hours.

Most of the rabid skunks were considered to be adults by the residents who submitted the animals. Since most of these skunks were reported during the spring, the distinction between adults and juveniles should have been pronounced. Among 32 striped skunks where even a general age class could be estimated on the basis of size, 31 were described as adults or "small adults." Only case 73-5 which was reported during August seemed to represent clinical rabies in a juvenile skunk. The single rabid fox occurred during December in an animal of adult size, but this animal could have been a young-of-the-year. The sex of rabid animals was rarely noted, and the only two observations were evenly divided with one male (case 76-6) and one female (case 74-3).

The general condition of the rabid animals as noted by the residents varied greatly. A frequent observation was that the animal was smaller than what they considered normal, but in a few cases the skunk was noted to be quite large. Some animals were described as noticeably emaciated, but again there were contrasting observations of rabid skunks which appeared to have been well-fed prior to death. One rabid skunk (case 76-7) was observed to be in extremely poor condition.

Only a few of the rabid skunks demonstrated any form of aggressive behavior. The three skunks which were found dead in the kennel area of confined dogs could have attacked these dogs. In several cases the skunk was initially seen fighting with dogs, and the residents often stated their belief as to whether the skunk attacked the dogs or vice versa. In cases 74-1, 76-2, 76-3, and 76-5, the skunk was considered by the residents to be the aggressor. In two cases (76-13 and 76-7) the skunks which had been wandering about the yard turned and moved directly toward the resident. These animals were both shot as they approached the resident, and no human exposures resulted.

The majority of rabid skunks discovered in the study area demonstrated nonaggressive behavior characterized by slow, disoriented movements. These animals appeared to be weak and uncoordinated. This general pattern was noted, in various degrees, among 19 of the 32 rabid skunks seen alive.

Many rabid skunks were initially detected by pet dogs. The rabid gray fox (case 76-15) might not have been discovered if several dogs had not attacked it. In some cases the rabid skunk appeared to be fleeing from attacking dogs.

The data from these interviews suggest that the detection of rabid skunks was not dependent on the chance discovery of the sick animal in its natural habitat, but that the rabid skunks which were reported moved into the living space of man in a highly visible manner. Many residents had a general understanding that the animals were demonstrating bizarre behavior, and most residents realized that these skunks were sick. In some cases the decision to seek a rabies diagnosis was reached in consultation with a local health official, a police officer, or a veterinarian. The fact that most of the rabid skunks were weak, disoriented, and detected initially by pet dogs greatly reduced the danger of humans being bitten by these skunks.

During the 1972-1976 period reported rabies cases were not uniformly distributed within the study area. The 46 cases with a known location occurred in only 15 of the 48 trap areas (Table 20). A completely uniform distribution would have resulted in rabies cases in 46 trap areas, and the

Table 20. Reported rabies cases among all species within the 48 trap areas of the study area, 1972-1976.[a]

Trap area	1972	1973	1974	1975	1976	Total	Trap area	1972	1973	1974	1975	1976	Total
1	-	3	2	-	-	5	25	-	-	-	-	-	-
2	-	2	-	-	-	2	26	-	-	-	-	-	-
3	-	-	-	-	1	1	27	-	-	-	-	-	-
4	-	-	1	-	-	1	28	-	-	-	-	-	-
5	-	-	-	-	-	-	29	-	-	-	-	-	-
6	-	-	-	-	-	-	30	-	-	-	-	-	-
7	-	-	-	-	-	-	31	-	-	-	-	-	-
8	1	-	1	-	-	2	32	-	-	-	-	-	-
9	-	-	-	-	-	-	33	-	-	-	-	-	-
10	-	-	-	-	-	-	34	3	-	-	-	1	4
11	-	-	-	-	-	-	35	-	-	-	-	1	1
12	-	-	-	-	-	-	36	-	-	-	-	-	-
13	-	-	-	-	-	-	37	-	-	-	-	-	-
14	-	-	-	-	-	-	38	-	-	-	-	-	-
15	-	-	-	-	-	-	39	4	-	-	-	-	4
16	-	-	-	-	-	-	40	2	-	-	-	2	4
17	-	-	-	-	-	-	41	-	-	-	-	-	-
18	-	-	-	-	-	-	42	1	-	-	-	-	1
19	-	-	-	-	-	-	43	1	-	-	-	4	5
20	-	-	-	-	-	-	44	2	-	-	-	4	6
21	-	-	-	-	-	-	45	-	-	1	1	-	2
22	-	-	-	-	-	-	46	4	-	-	-	2	6
23	-	-	-	-	-	-	47	-	-	-	-	2	2
24	-	-	-	-	-	-	48	-	-	-	-	-	-
Total	1	5	4	0	1	11		17	0	1	1	16	35

[a]Partial data available for 1972 (18 of 24 reported cases).

observed pattern differed from such a uniform distribution in a highly significant manner ($P < .001$). Approximately 70 percent (32/46) of all reported rabies cases of known location occurred in 15 percent (7/48) of the trap areas. These trap areas were 1, 34, 39, 40, 43, 44, and 47.

One interesting aspect of the rabies situation in Greene County was the recurrence of the first, or only, rabies case during the years of the study in the same part of the county. The first two rabies cases during 1972 occurred approximately 3.5 km apart in the northern part of the county (trap area 46). The county was free of reported rabies cases during 1973, but in 1974 the single case of skunk rabies occurred less than 6.5 km west of the two earliest cases of 1972. The single case of horse rabies during 1975 was approximately 5 km north of the 1974 case and 12 km west of the two earliest rabies cases of 1972. Rabies case 76-2 was located about 1 km from the site of rabies case 72-1, and rabies case 76-1 was approximately 6.5 km east of rabies case 76-2. Therefore, in Greene County which contains almost 1,600 km^2, the earliest reported rabies cases for four years all occurred in a narrow strip of land approximately 16 km in length near the northern corner of the county.

A similar situation existed in Jefferson County during the 1973-1976 period. In the northwestern part of the county the initial cases during 1973 and 1974 were separated by less than 6.5 km. The rabid gray fox which was reported during December 1976 was located approximately 9 km from rabies case 73-1 and 11 km from rabies case 74-1.

Using the trap area as the unit of reference, the recurrence patterns for the reported rabies cases among all species from 1972 through 1976 are given in Table 21. The strongest positive association was between the cases in 1972 and those in 1976. The recurrence patterns among the counties of the study region during the years characterized by skunk rabies (Table 12, page 64) indicated that the greatest similarity among the counties reporting rabies cases occurred at intervals of two and four years. There is a slight suggestion of such a pattern among the trap areas of the study area based on the reported cases of 1972, but an outbreak which might have been expected during 1974 did not occur.

The general recurrence pattern of reported rabies cases in Jefferson County differed from that observed in Greene County. The only rabid skunks reported in Jefferson County occurred during two consecutive years, 1973-1974, and no rabid skunks were reported in the county during the final two years of the study. However, Greene County reported rabid skunks during six of the eight years from 1969 through 1976 with noticeable upsurges during 1969, 1972, and 1976.

Table 21. The recurrence pattern for reported rabies cases (all species) among the 48 trap areas of the study area, 1972-1976.[a]

	1973 (2)	1974 (4)	1975 (1)	1976 (8)
1972 (8)	-0.09	+0.07	-0.06	+0.55
1973		+0.31	-0.30	-0.09
1974			+0.48	-0.14
1975				-0.06

	Average recurrence coefficient for analogous years
+3 years	-0.08
+2 years	-0.12
+1 year	+0.16

[a]The degree of association is expressed by the point correlation coefficient which ranges from +1 for totally identical patterns to -1 for total dissimilarity. Numbers in parentheses are the number of trap areas containing rabies cases during the year.

III. ANIMAL POPULATION CHARACTERISTICS

Results of the Trap Effort

The live trapping of animals in the study area extended from 1973 through 1976. During this time 1,278 animals were captured (Table 22). The most frequently captured animals were opossums and free-roaming domestic cats. These two animals constituted 92 percent (1,181/1,278) of all captures. The 15 rat-like rodents captured during the study were primarily cotton rats (*Sigmodon hispidus*), and other rodents included one eastern chipmunk (*Tamias striatus*) and one woodchuck. The seven birds included two cardinals (*Richmondena cardinalis*), two crows (*Corvus brachyrhynchos*), a bobwhite quail (*Colinus virginianus*), a ruffed grouse (*Bonasa umbellus*), and a grackle (*Quiscalus quiscula*). The 57 turtles were all eastern box turtles (*Terapene carolina*). Four of the five domestic dogs captured appeared relatively tame and the fifth did not appear vicious.

Opossum Population Characteristics

The 793 opossum captures represented 62 percent (793/1,278) of all the animals captured. The relative abundance and distribution of opossums were considered in reference to each of the 48 trap areas. The relative abundance was expressed by a capture rate, the calculated number of captures per 100 trap night. The distribution, or dispersion, within a trap area was expressed by the percentage of sites used in

Table 22. Trap effort and animals captured in the study area, 1973-1976.

	1973 Number	1974 Number	1975 Number	1976 Number	Total
Trap nights	2,235 (34/-)[a]	2,161 (33/-)	1,688 (25/-)	548 (9/-)	6,632
Trap sites used	794 (34/-)	744 (32/-)	626 (26/-)	195 (8/-)	2,359
Captures					
Striped skunk	0	2 (67/ 1)	0	1 (33/ 1)	3 (-/ *)
Opossum	170 (21/52)	195 (25/62)	314 (40/68	114 (14/65)	793 (-/62)
Cat	130 (34/40	98 (25/31)	117 (30/25)	43 (11/24)	388 (-/30)
Raccoon	1 (25/ *)	0	3 (75/ 1)	0	4 (-/ *)
Dog	0	0	4 (80/ 1)	1 (20/ 1)	5 (-/ *)
Rabbit	2 (50/ 1)	1 (25/ *)	0	1 (25/ 1)	4 (-/ *)
Rodents "rats"	7 (47/ 2)	7 (47/ 2)	1 (7/ *)	0	15 (-/ 1)
Birds	0	6 (86/ 2)	0	1 (14/ 1)	7 (-/ 1)
Turtles	15 (26/ 5)	5 (9/ 2)	22 (39/ 5)	15 (26/ 8)	57 (-/ 4)
Other mammals	1 (50/ *)	0	0	1 (50/ *)	2 (-/ *)
Total	326 (26/-)	314 (25/-)	461 (36/-)	177 (14/-)	1,278

[a](A/B) = (percentage of horizontal row total/percentage of column total).

* = Less than 0.05%.

the trap area which yielded one or more opossums, the site success rate. The capture rates and site success rates among the 48 trap areas in regard to opossums are presented in Appendix K for the four-year period of 1973-1976.

During 1973 a total of 170 opossums were captured in 47 of the 48 trap areas. The capture rates ranged from 0 in trap area 9 to 19.4 in trap area 31. The capture rate for the entire study area was 7.5. Opossums appeared to be widely dispersed throughout the study area. The site success rates ranged from 0 in trap area 9 to 40.7 in trap area 35, and the site success rate for the entire study area was 19.8. Opossums appeared to be more abundant and widely dispersed in trap areas 25-48 than in trap areas 1-24, but the difference in abundance was not significant ($P > .05$).

During 1974 there were 195 opossum captures in 46 trap areas and the two farms. Among the trap areas the capture rates ranged from 0 in trap areas 21 and 36 to 22.2 in trap area 11. The capture rate for the entire study area was 9. The site success rates ranged from 0 in trap areas 21 and 36 to 53.8 in trap area 10. The site success rate for the study area was 22.8. The capture rates and site success rates among the two major divisions of the study area were remarkably similar.

During 1975 there were 314 opossum captures, and for the first time opossums were captured in all of the 48 trap areas. The capture rates ranged from 3.1 in trap area 26 to

34.9 in trap area 9. It is interesting to note that no opossums were captured in trap area 9 during August 1973 with a trap effort of 35 trap nights, but in August 1975 the same trap effort yielded 12 opossums. The capture rate for the entire study area was 18.6, a rate which was more than twice the capture rate found in either 1973 or 1974. The site success rate for the study area in 1975 was 42.2 which was also much higher than the rates of either 1973 or 1974. These rate increases may not have resulted from an increase in the opossum population due to the fact that trapping during 1975 was done primarily at established sites, and many of the less productive sites were excluded. The capture rates and site success rates of the two sections of the study area were again similar.

The roadside trap effort during 1976 was not random but highly selective for those sites which had yielded opossums in previous years, primarily rabies seropositive opossums. Forty-one percent (223/548) of the trap nights used during 1976 were on farms from which rabid animals had been reported during 1976. During the two months of trapping in 1976, 114 opossums were captured for an overall capture rate of 20.8 and a site success rate of 42.6. Both of these rates were higher than those found in previous years.

Considering all the data gathering in roadside trapping during the 1973-1976 period, opossums were both abundant and widely distributed throughout the study area

(Table 23). Among the 48 trap areas, capture rates for the four-year period ranged from 5.0 in trap area 24 to 19.4 in trap area 1. The site success rates ranged from 20 in trap area 26 to 60 in trap areas 10 and 32. Trap areas 24 and 26 were both in the southern part of the study area and contained large areas of mountainous forest. Trap areas 1, 10, and 32 were in the valley region and contained primarily small wooded ridges and woodlots interspersed with agricultural land.

Of the 793 opossums captured during the four years of the study, 689 were collected for serological and/or ecological study (Table 24). Females constituted 62 percent (430/689) of the opossums collected and this preponderance of females was highly significant ($P < .001$). Petrides (1949:375) reviewed the data on the sex ratios found in several studies on opossums, and in most cases there was a preponderance of males which composed from 54 to 57 percent of the population. Similar data were presented by Llewellyn and Dale (1964:120) who found that males composed 54 percent (118/220) of the opossum population examined in Maryland. Other studies have found opossum populations to be fairly evenly divided among males and females (Fitch and Sandidge 1953:331-332, Stout and Soneshine 1974a:240). While the apparent majority of females among opossums in the study area could have been an artifact of the trapping procedure, any ecological factors responsible for such an unbalanced sex ratio could not be determined.

Table 23. Relative abundance and distribution of opossums at roadside sites in the 48 trap areas as expressed by capture rate, opossums captured per 100 trap nights (TN), and percentage of sites used which yielded one or more opossums, 1973-1976.

Trap area	Number of		Cap-ture	Trap sites			Trap area	Number of		Cap-ture	Trap sites		
					With capture(s)							With capture(s)	
TA	TN	Opossums captured	rate	Used	Number	%	TA	TN	Opossums captured	rate	Used	Number	%
1	186	36	19.4	32	14	43.8	25	144	8	5.6	32	7	21.9
2	156	11	7.0	27	7	25.9	26	103	7	6.8	20	4	20.0
3	150	14	9.3	28	11	39.3	27	145	19	13.1	35	10	28.6
4	143	16	11.2	29	8	27.6	28	92	14	15.2	27	9	33.3
5	139	22	15.8	38	15	39.5	29	137	18	13.1	26	11	42.3
6	149	11	7.4	29	9	31.0	30	110	12	10.9	26	9	34.6
7	108	16	14.8	26	10	38.5	31	143	23	16.1	28	13	46.4
8	143	14	9.8	32	11	34.4	32	105	19	18.1	25	15	60.0
9	106	17	16.0	24	10	41.7	33	132	11	8.3	30	9	30.0
10	141	25	17.7	25	15	60.0	34	144	13	9.0	30	10	33.3
11	162	23	14.2	28	11	39.3	35	175	30	17.1	29	16	55.5
12	134	12	9.0	29	6	20.7	36	105	13	12.4	28	10	35.7
13	141	10	7.1	29	9	31.0	37	113	14	12.4	26	8	30.8
14	104	15	14.4	21	9	42.8	38	92	12	13.0	24	7	29.2
15	96	15	15.6	25	9	36.0	39	113	17	15.0	26	6	23.1
16	120	17	14.2	26	11	42.3	40	168	21	12.5	32	8	25.0
17	107	9	8.4	25	7	28.0	41	101	9	8.9	28	7	25.0
18	92	11	12.0	23	7	30.4	42	106	17	16.0	25	13	52.0
19	100	13	13.0	24	6	25.0	43	151	16	10.6	35	8	22.8
20	156	12	7.7	29	9	31.0	44	173	23	13.3	31	11	35.5
21	104	9	8.6	30	8	26.7	45	174	17	9.8	29	10	34.5
22	143	17	11.9	36	12	33.3	46	162	21	13.0	33	11	33.3
23	107	9	8.4	25	7	28.0	47	132	14	10.6	28	9	32.1
24	139	7	5.0	34	7	20.6	48	167	25	15.0	31	11	35.5
Subtotal	3,126	361	11.5	674	228	33.8		3,187	393	12.3	684	232	33.9
			Study area total (TA 1-48)					6,313	754	11.9	1,358	460	33.9

Table 24. Monthly composition of the opossum population collected in the study area by age class, weight class, and sex, 1973-1976.[a]

Age class	Juvenile				Subadult		Adult										
Age in months[b]	4.0- 4.7		4.7- 6.5		6.5 8.5		8.5 10.2		10.2 11.0+		Over 12						
Weight class	1		2		3		4		5		6		7				
Weight (kg) More than or equal to:	0.23		0.45		0.91		1.36		1.82		2.27		2.72		Total By sex		
Less than:	0.45		0.91		1.36		1.82		2.27		2.72		4.10				
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
February	0	0	0	0	0	1	0	4	2	0	1	0	2	0	5	5	10
% Feb.	0		0		10		40		20		10		20		50	50	
March	0	0	0	0	0	2	1	9	5	6	9	2	0	1	15	20	35
% Mar.	0		0		6		29		31		31		3		43	57	
April	0	0	0	0	0	0	2	6	5	8	11	7	5	3	23	24	47
% Apr.	0		0		0		17		28		38		17		49	51	
May	12	7	0	0	1	2	1	43	14	40	20	8	8	3	56	103	159
% May	12		0		2		28		34		18		7		35	65	
June	3	2	7	8	0	0	1	14	4	28	6	13	8	0	29	65	94
% June	5		16		0		16		34		19		9		31	69	
July	0	0	17	9	16	11	3	7	3	18	3	15	6	6	48	66	114
% July	0		23		24		9		18		16		10		42	58	
August	2	1	5	0	11	11	6	17	3	24	1	12	2	2	39	67	97
% Aug.	3		5		23		24		28		13		4		31	69	

Table 24. continued.

Age class	Juvenile				Subadult		Adult										
Age in months[b]	4.0-4.7		4.7-6.5		6.5-8.5		8.5-10.2		10.2-11.0+		Over 12						
Weight class	1		2		3		4		5		6		7				
Weight (kg)															Total		
More than or equal to:	0.23		0.45		0.91		1.36		1.82		2.27		2.72		By sex		
Less than:	0.45		0.91		1.36		1.82		2.27		2.72		4.10				
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
September	1	12	7	1	3	16	19	16	10	22	4	6	4	2	48	75	123
% Sept.	11		6		15		28		26		8		5		39	61	
October	0	0	1	0	1	1	1	2	1	1	1	1	0	0	5	5	
% Oct.	0		10		20		30		20		20		0		50	50	
Total	18	22	37	18	32	44	34	118	47	147	56	64	35	17	259	430	689
% Total	6		8		11		22		28		17		8		38	62	

[a]Weights of lactating females include pouch young.

[b]All ages are approximations and based on weight-age data given by Petrides (1949:371).

Captured opossums were assigned to one of seven weight classes. The first six weight classes contained increments of .45 kg (1 lb) and the seventh weight class contained an increment of 1.38 kg (3 lbs) in order to consider all the heavier animals as a single group.

Based upon weight and probable age, the captured opossums were assigned to one of three age classes. The relationship between weight and age for opossums weighing less than 2 kg was based on data given by Petrides (1949:371). The first two weight classes contained opossums weighing less than 0.91 kg. These opossums were readily recognized as young-of-the-year and designated as juveniles. There was some ambiguity associated with the opossums weighing more than 0.91 kg but less than 1.36 kg, weight class 3. During February and March the opossums in weight class 3 were not young-of-the-year, and one female captured on 2 March 1974 had pouched young and the combined weight of mother and young was 1.2 kg. However, during the fall opossums in weight class 3 were often clearly distinguishable as young-of-the-year. Females captured during September and weighing less than 1.36 kg normally had pouches with white, downy fur which is characteristic of nulliparous females (Petrides 1949:371) and strongly suggestive that the animals had been born earlier that year. Therefore, the subadult class, as used in this study, does not imply sexual immaturity in all cases, but refers to those opossums which are not yet fully grown.

These subadults were considered to be from 6.5 to 8.5 months of age. A large majority of the opossums weighing more than 1.36 kg, weight classes 4-7, were probably in their second calendar year of life, and were, for the most part, fully grown. While some young-of-the-year males may have reached weight class 4 during late September, those opossums weighing more than 1.36 kg were considered to be adults and may have included individuals in their second or third year of life.

The data in Table 24 indicate that opossums in the study area produce two litters of young per year. Very young opossums were captured during the May-June period and again during the August-September period. The first breeding season seemed to occur in late January or early February. All five females captured from 14 February to 22 February 1974 had young in their pouches. The second breeding season must begin soon after the young of the first litter become independent, probably in late April or May. Many females were carrying young during July, but by August practically none of the adult females had pouched young. However, one female captured on 16 August 1976 did have two pouched young.

The data in Table 24 also provide information on changes in the age structure of the opossum population during the year. The early spring (February-March) population was composed primarily of adults with approximately 6 to 10 percent subadults which were probably members of the second litter from the previous year. After the young of the first litter became independent, the population contained slightly over 20 percent juveniles during the June-July period. By the August-September period the opossum population contained over 30 percent nonadults. In October many young-of-the-year had probably reached the weight criterion of subadults, and the two nonjuvenile age classes contained 90 percent of the population.

Few data were available to directly assess any fluctuations of the opossum population over the years of the study. While the capture rate for opossums in the study area increased during each year of trapping, there was an exclusion of some less productive sites as the study progressed. The best indicator of population fluctuations was the capture data from the 38 trap sites which were used during all four years. From 1973 to 1976 these 38 sites were used for 79, 80, 74, and 80 trap nights, respectively. The number of opossums captured at these sites was, in sequence, 17, 21, 15, and 13. These values suggest that the opossum population was relatively stable, and it is doubtful that any major changes occurred in the population of opossums when the study area is considered as a whole.

Free-Roaming Cat Population Characteristics

Free-roaming domestic cats ranked second in number of captures. Thirty percent (388/1,278) of all animals captured were cats. The extent to which these cats were truly feral was not determined, but the majority appeared to be extremely vicious and fled rapidly away from the trap site upon release. Data on the capture rates and site success rates among the 48 trap areas in regard to cats are presented for each year in Appendix L.

There were 130 cats captured during 1973 in 42 of the 48 trap areas. The capture rates ranged from 0 in trap areas 4, 15, 23, 24, 25, and 38 to 13.9 in trap areas 12 and 17. The site success rates ranged from 0 to 41.7. Within the study area the capture rate was 5.8 and the site success rate was 13.4. Both of these figures were slightly less than those found for opossums during 1973.

During 1974, 98 cats were captured in 40 of the 48 trap areas. The trap areas with no captures were 4, 5, 13, 15, 23, 25, 29, and 47. Cats were most abundant in trap area 8 which had a capture rate of 14.3 and a site success rate of 41.7. Within the study area the capture rate was 4.5 and the site success rate was 12.1. These figures are less than those for cats during 1973 and approximately half of the respective rates found among opossums during 1974. On 25 March 1974 a cat was captured at a site in trap area 46 which was the site of a striped skunk capture two days later.

During 1975 there were 117 cat captures in 44 trap areas. The trap areas with no captures were 6, 22, 30, and 36. Cats were most abundant in trap area 38 which had a capture rate of 16.7 and a site success rate of 50. Within the entire study area the capture rate was 6.9 and the site success rate was 17.4. Both of these figures are higher than those for cats in the two previous years, but much lower than the figures for opossums during 1975.

During 1976, 43 cats were captured in 13 of the 15 trap areas used and on five of the eight farms used. Cats were not captured in trap areas 11 and 39 or on Farms H, GO, and V. The highest capture rate was 41.4 on Farm W, and the single site used in trap area 34 yielded a cat. The overall capture rate was 7.8 and cats were captured at 20 percent (39/195) of the trap sites.

During the 1973-1976 period cats were captured in all 48 trap areas and on seven of the 10 farms. The trap areas with the fewest captures were trap areas 4, 15, and 24 (two cats), and trap areas 23, 25, and 36 (three cats). Trap areas 23-25 are in the mountainous forest area of the southern part of the study area. Trap areas 4, 15, and 36 are in the valley region and are characterized by wooded ridges and small woodlots interspersed with agricultural land. Large numbers of cats were captured in trap areas 8, 43, and 44 (15 cats) and trap area 45 (17 cats). These four trap areas are in the valley region. Cat captures were not noticeably more frequent in areas of high human population.

Cats were sampled serologically only during 1975. In that year data were collected from 57 cats. These cats were rather evenly divided between males (26) and females (31).

Cats were not assigned to specific age classes, but those sampled all appeared to be adults or subadults. The smallest cat, a female captured on 24 August, weighed 1.7 kg. The largest cat, a male captured on 4 September, weighed 4.8 kg.

Based on data from the 38 trap sites which were used during all four years, there did not appear to be any significant fluctuation in the population density of free-roaming domestic cats. During these years there were 6, 3, 7, and 7 cat captures at these sites, respectively. While there may have been fewer cats in the area during 1974, the trap effort during that year (February-June) started earlier than trapping in the other three years and the captures during 1974 may have been lower for this reason. The population of free-roaming domestic cats, therefore, appeared to be relatively stable during the study.

Striped Skunk Population Characteristics

The striped skunk was unquestionably the dominant species among reported rabies cases during the study period. This fact dictated a thorough analysis of the striped skunk population in the counties of the study area. However, in spite of the fact that 25 rabid striped skunks were reported in the study area from 1973 through 1976, the basic characteristics of the striped skunk population were extremely difficult to evaluate.

One salient fact was the extremely low capture rate of skunks in relation to opossums and free-roaming domestic cats. There was a total of 1,181 captures among the two latter species which contrasts sharply with the three striped skunk captures (Table 25). These three striped skunks were all males, and two were adults. The fact that the first two skunk captures occurred at sites which also yielded an opossum and cat, respectively, suggests that the areas used for foraging by these three species may overlap. The use of the same area by opossums and striped skunks was demonstrated by Shirer and Fitch (1970:493), and a spatial overlap among opossums, striped skunks, and feral cats was noted by Andrews and Ferris (1966:133). The fact that opossums and skunks, primarily striped skunks, can inhabit the same area is reflected by data from studies in which both animals were captured (Table 26). These data show a skunk:opossum capture ratio which varies from 1:0.87 to 1:2.42. Clearly, the ratio found in the present study, 1:264, is out of line with data from other studies, but any procedural or ecological reasons for such a disparity are unknown.

In December 1973 a test was conducted to evaluate the trapping procedure in an area known to have a large striped skunk population. In conjunction with another wildlife study, nine traps were placed in the Cades Cove section of the Great Smoky Mountains National Park. These traps were left in place over two nights, and the 18 trap nights produced the capture

Table 25. Data on striped skunks captured in the study area, 1973-1976.

Date of capture	Location: Trap area, quadrant	Age class	Sex	Weight (kg)	Length (cm): Body	Length (cm): Total	Site description	Other observations
14 Feb. 1974	41 SW	Adult	M	2.0	43.2	76.2	Edge of small stream in woodlot adjacent to pasture	The opossum captured 2 nights later was presumptive rabies seropositive
27 March 1974	46 SE	Adult	M	1.4	38.1	71.1	Thin fence-row by short grass pasture	Located approximately 4.8 km from rabies case 74-3 and 2.0 km from rabies case 76-2. Many ticks on head, bare patch of skin on shoulder.
20 July 1976	Farm M (TA 44)	Juvenile	M	0.6	27.9	45.7	Small woodlot surrounded by pasture and cropland	Located approximately 100 m from site of rabies cases 76-6 (June 7)

Table 26. Examples of skunk:opossum capture ratios in selected studies compared with data from the present study.

Location	Time period	Number of captures: Skunk	Number of captures: Opossum	Capture ratio Skunk:Opossum	Source
Georgia, Florida, S. Carolina	4 years	144[a]	215	1 : 1.49	Wood and Davis 1959:123
Alabama	___	100[b]	127	1 : 1.27	Sikes 1962: 1047
Virginia	11 months	1,696[b]	977	1 : 0.58	Marx and Swink 1963:174
Illinois	3 years	120[a]	143	1 : 1.19	Verts 1967:157
Illinois	18 months	79[a]	94	1 : 1.19	Andrews and Ferris 1966:132
Tennessee	10 months	43[a]	104	1 : 2.42	Mahon 1973:76
Iowa	15 months	87[a]	95	1 : 1.09	Niemeyer 1973:13
Virginia	6 years	31[a]	72	1 : 2.32	Stout and Sonenshine 1974a:240 1974b:140
Tennessee (Great Smoky Mountains National Park)	16 months	62[b]	54	1 : 0.87	Dr. M. R. Pelton (personal communication)
Present study	4 years	3[a]	793	1 : 264	

[a]Striped skunks only.

[b]Species composition of skunks not given.

of two adult striped skunks. The bait, distance from the road, and general trap setting were similar to procedures used in the study area.

The trapping procedures used in the study area were not considered to be biased against the capture of skunks. Most traps were set along roads which had light traffic during the day, and practically none at night. Skunks are often found along country roads in search of carrion (Caras 1967:213). In many cases these roads followed the course of a small stream, and traps were placed in wooded areas along these streams. Andrews and Ferris (1966:132) noted the preference of striped skunks for areas along waterways. Several study area sites were in shrubby fencerows bordering cornfields, and such areas were considered good feeding sites for striped skunks (Verts 1967:83). Storm (1972:38-39) noted that fencerows might be important to striped skunks as a location for den sites.

Allowing the traps to remain in place for three consecutive nights should have been adequate to attract skunks foraging in the immediate vicinity. In a skunk rabies study in Illinois, the traps remained in place for four nights (Verts 1967:6), and in a study of Ohio skunks (Bailey 1971: 197) the traps were moved regularly in order to distribute the trapping effort.

It is possible that the greater population density of opossums and cats, as suggested by the capture data, could have enabled individuals of these species to reach the trap sites prior to striped skunks and thereby prevented skunks from being captured. However, the study called for captured opossums to be killed, and cats which were captured once rarely returned to the trap site. After the capture and removal of opossums and the release of cats, there was apparently an opportunity for skunks in the study area to approach the undisturbed traps.

Striped skunks were observed as road-kills, captured, or submitted for a rabies diagnosis in 48 percent (23/48) of the trap areas. Some striped skunks were noted in each of the three counties. The trap areas without any evidence of striped skunks were primarily those in the mountainous forest areas of southern Cocke County and southeastern Greene County. Striped skunks within the study area were divided into two groups. One group contained those striped skunks found to have clinical rabies by laboratory diagnosis. The second group contained all other striped skunks. The latter group, designated as skunks not associated with reported skunk rabies cases, contained (1) striped skunks observed as road-kills, (2) skunks captured during the trap effort, and (3) skunks submitted to the health department and diagnosed negative for rabies. Except for the skunks in the latter category which were considered to be nonrabid, the study made no assumptions regarding the incidence of clinical rabies among the skunks not associated with reported skunk rabies cases. Burkel et al. (1970:499) found that 26 percent of 61 striped skunks collected as road-killed carcasses less than one day after death were rabies infected. The three striped skunks captured during the study did not exhibit any abnormal behavior suggestive of the furious type of clinical rabies. Therefore, it is likely that the majority of the skunks not associated with reported skunk rabies cases were not clinically rabid, although the extent of subclinical rabies infection among these skunks could not be determined.

There were 17 striped skunks located within the study area among the three categories which contained skunks not associated with reported skunk rabies cases. These 17 skunks were located in 15 trap areas (Fig. 21). Only two striped skunks which were submitted for a rabies diagnosis and found to be negative could be located. The residents submitting these animals considered the skunks to be of adult size, but there was no information regarding the sex of these striped skunks. One striped skunk was submitted in April 1976 and was located in trap area 40. The other striped skunk was submitted in March 1977 and was located in trap area 39 near Greeneville.

Nineteen road-killed striped skunks were observed during the travel associated with the trap effort, but only 12 of these were located in the study area (Table 27). The seven road-kills located in the southern part of Hamblen County were all observed along an approximately 20 km section

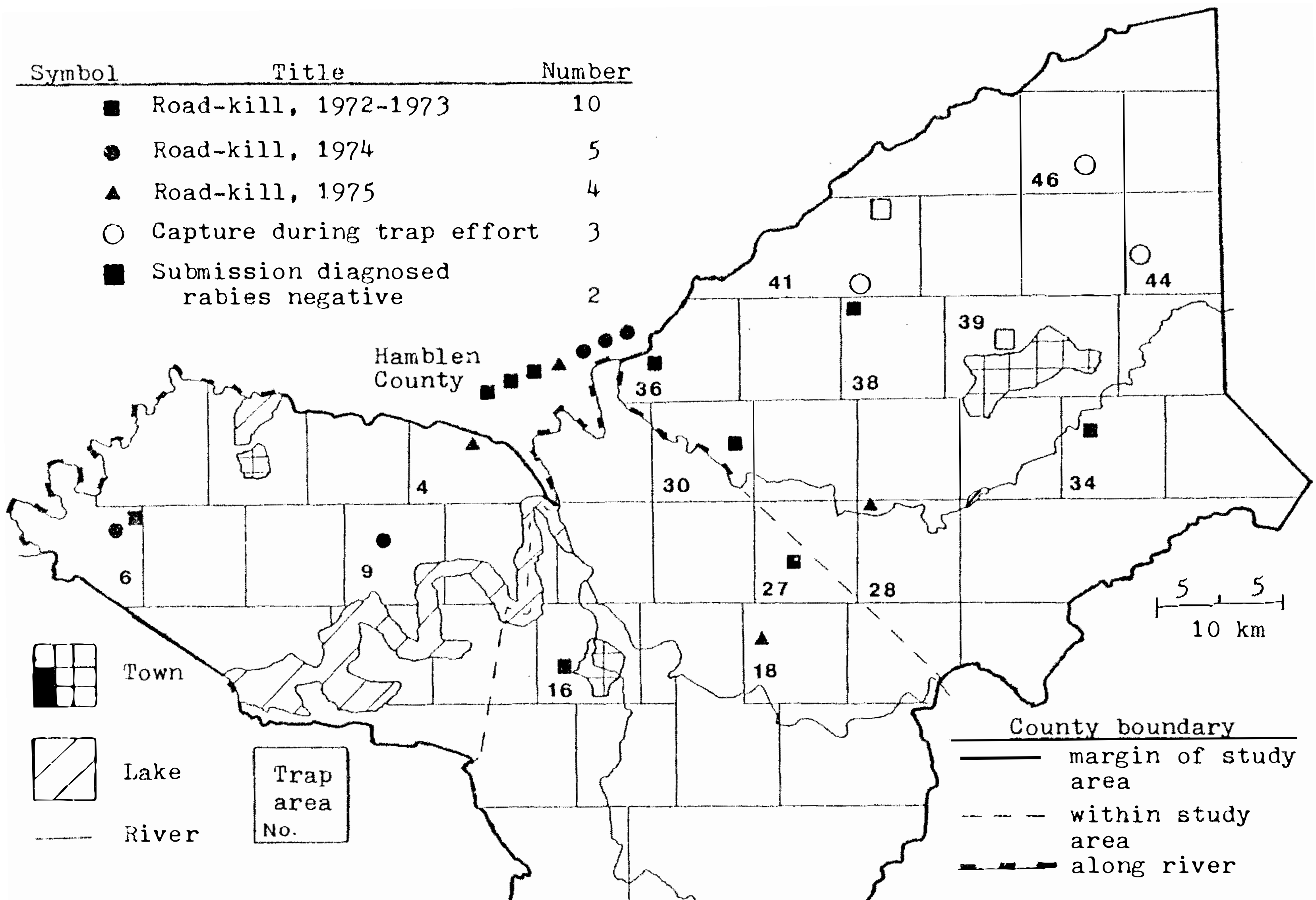


Fig. 21. Distribution of striped skunks not associated with reported skunk rabies cases in the study area and Hamblen County, 1972-1977.

Table 27. Location, date, and biological characteristics of road-killed striped skunks observed in the study area and adjacent Hamblen County.

Month year		Approximate distance driven (km)	Number of road-kills seen	Day of month	Location: County	Location: Trap area-quadrant	Age class[a]	Sex
Oct.	72	*	1	22	Greene	34-NW	Ad.	Male
May	73	2,720	0					
June	73	2,250	1	14	Cocke	27-SE	Ad.	Female
July	73	2,220	2	25	Cocke	16-SE	*	Female
				25	Greene	30-NE	Ad.	Female
Aug.	73	2,300	4	8	Greene	38-NW	*	*
				14	Jefferson	6-NE	Juv.	*
				14	Hamblen		*	*
				21	Greene	36-SW	*	*
Sept.	73	2,650	2	12	Hamblen		Ad.	*
				13	Hamblen		Ad.	*
Oct.	73	690	0					
Feb.	74	1,350	3	13	Hamblen		Ad.	Male
				14	Hamblen		*	*
				14	Hamblen		*	*
Mar.	74	2,830	1	1	Jefferson	9-NW	Ad.	*
Apr.	74	3,310	0					
May	74	3,330	1	30	Jefferson	6-NE	Ad.	Female
June	74	260	0					
May	75	2,990	2	14	Hamblen		Ad.	Male
				18	Greene	28-NW	Ad.	Male
June	75	2,910	0					
July	75	1,670	0					
Aug.	75	1,050	1	26	Jefferson	4-NE	*	*
Sept.	75	2,980	1	10	Cocke	18-SW	Ad.	Male
July	76	1,270	0					
Aug.	76	2,800	0					
Total		39,580	19					

[a]Age class based on an evaluation of body size.

*Data not available.

of interstate highway which extends into both Jefferson and Greene counties. The fact that over a third of all the road-killed striped skunks were observed in Hamblen County suggests that this area outside the study area had a larger population of striped skunks than the three counties of the study area. The age class assigned to these road-kills was based upon size alone, but the fact that many of these animals were observed during the summer months when the distinction between young-of-the-year and adults should be pronounced suggests that these age designations were accurate. The sex ratio among road-killed striped skunks was not greatly divergent from unity (5 males:4 females). There was no observation of road-killed spotted skunks during the study.

The limited data from the 17 striped skunks not associated with reported skunk rabies cases were not sufficient to evaluate any population fluctuations which may have influenced the periodicity of skunk rabies cases in the study area. However, data were available on the number of skunk pelts purchased by a fur dealer in Hamblen County from the fall of 1965 through the spring of 1977. The data prior to the 1972-1973 season was based primarily on records kept by the dealer. From the fall of 1972 through the spring of 1977, the number of pelts purchased by this dealer was based primarily on data supplied by the Tennessee Wildlife Resources Agency in Nashville, Tennessee.

The use of data on the number of animals collected by fur trappers as a measure of population fluctuations is, at best, a poor index. These data were examined for only the most general trends which might suggest the relationship between the abundance of skunks and the incidence of reported skunk rabies cases. Because the majority of the pelts purchased by the dealer in Hamblen County came from trappers in that county and the five counties adjacent to it, the number of reported skunk rabies cases in this six-county area was considered. These data refer to skunks without distinguishing between striped and spotted skunks. However, the data from the study area indicate that none of the skunk rabies cases investigated during the study were among spotted skunks. Warren (1975:27, 53) noted that the spotted skunk in Tennessee is an insignificant fur animal. Therefore, there is reason to believe that these data on skunk rabies cases and skunk pelt purchases are, for the most part, in regard to the striped skunk. The relationship between the number of skunk pelts purchased and the number of reported skunk rabies cases is shown in Fig. 22. Both sets of data contain very low numbers in relation to the large area considered, but several interesting trends are suggested.

The number of skunk pelts sold by trappers declined steadily from the 1965-1966 season to the 1968-1969 season. During the four years from 1965 through 1968, only one rabid skunk was reported in the six-county unit, and this skunk rabies case occurred in Grainger County. While Hawkins County

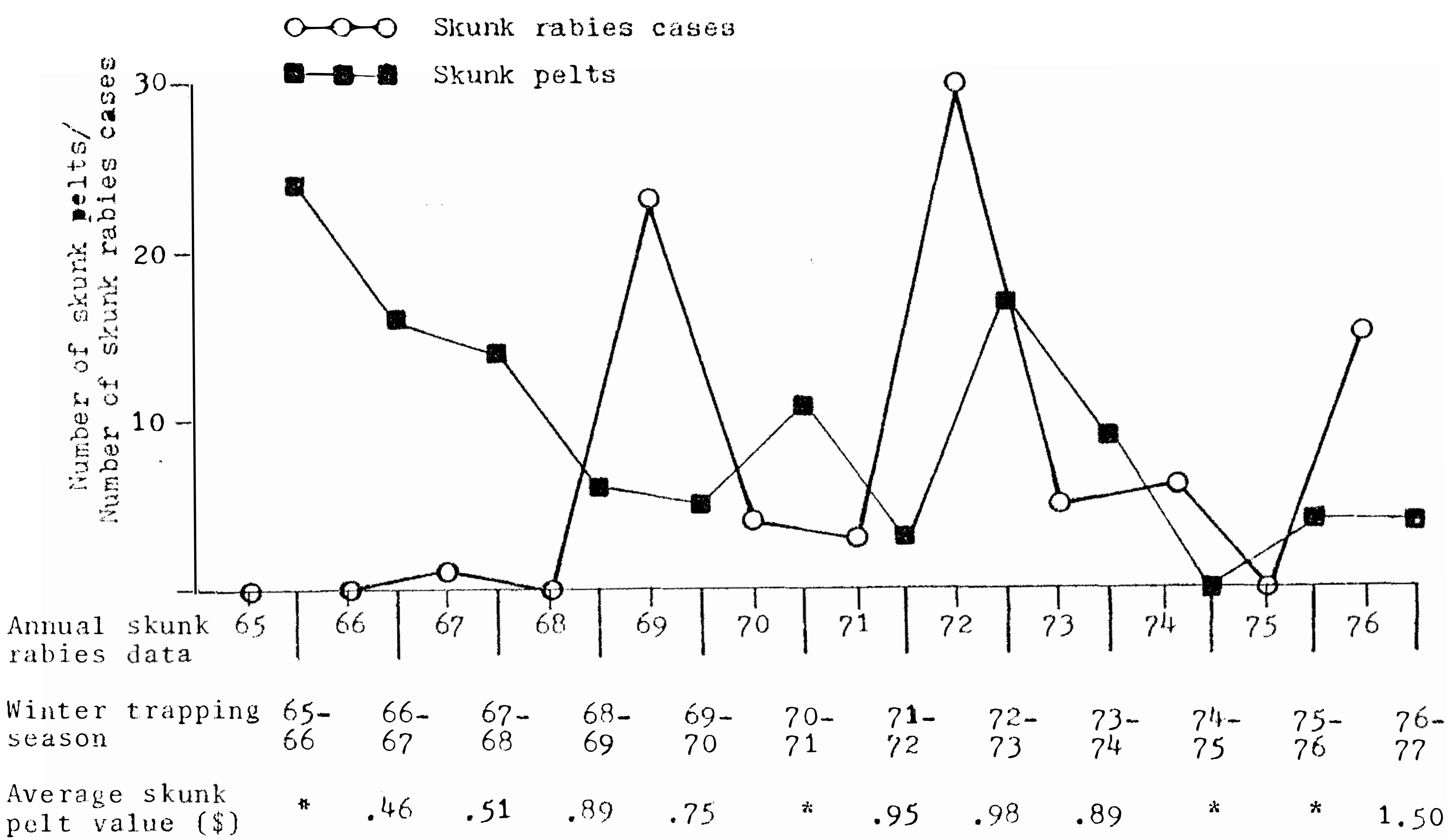


Fig. 22. Number of skunk pelts purchased by a Hamblen County fur dealer during the winter (November-March) trapping season, 1965-1977, and the number of rabid skunks reported from Hamblen County and five contiguous counties (Greene, Cocke, Jefferson, Hawkins, and Grainger), 1965-1976. *Data not available.

extends farther north than Grainger County, the latter does lie just south-southwest of Hancock County (Figure 1, page 11). Therefore, the idea of a southward progression of rabies infection among skunks is a viable hypothesis.

During 1969 there were 30 reported rabies cases in the six-county unit, and 23 of these cases were among skunks. Sixty percent (18/30) of these cases occurred in the April-October period which was after the 1968-1969 trapping season and before the 1969-1970 trapping season.

During the two years (1970-1971) following the 1969 outbreak, rabid skunks continued to occur sporadically. During this period the number of skunk pelts sold by trappers increased (1970-1971 season) and then decreased (1971-1972 season). In 1972 the six-county unit experienced a second upsurge of skunk rabies cases with 32 reported cases, 30 skunks and two cows (see Appendix G). Sixty-six percent (21/32) of these cases occurred in the months of March and April, after the bulk of the 1971-1972 trapping season. As seen in the 1969 outbreak, the number of skunk pelts sold by trappers was lower in the winter immediately preceding the outbreak than the winter approximately one year prior to the outbreak. In the winter immediately following the 1972 outbreak (1972-1973 season), the number of skunk pelts collected by trappers increased from the number sold in the winter preceding the outbreak.

Following the 1972-1973 trapping season the number of skunk pelts sold by trappers decreased for two consecutive seasons in the presence of moderate levels of reported skunk rabies cases during 1973 (five cases, all in Jefferson County) and 1974 (six cases). During the 1974-1975 trapping season, no skunk pelts were sold by trappers. Based on the data from previous years a rise in the number of skunk pelts sold would have been expected during the 1974-1975 trapping season. It is interesting to note that the total absence of skunk pelts during the 1974-1975 season immediately preceded the year, 1975, with the lowest number of recorded rabies cases (3) in the study region during any year for which data are available (Table 10, page 55). During 1975 there were no reported cases of skunk rabies in the six counties.

Based on the occurrence of skunk rabies outbreaks during 1969 and 1972, an outbreak might have been expected during 1975. Instead, the upsurge of reported skunk rabies cases occurred during 1976 when 15 skunk rabies cases were reported in Greene County. This 1976 upsurge followed a slight increase in the number of skunk pelts sold by trappers.

While realizing all the limitations of the data presented in Fig. 22, several patterns did appear during this period. Noticeable peaks in the number of reported skunk rabies cases were separated by three or four years. The winters preceding the outbreaks of 1969 and 1972 were not characterized by higher than normal captures of skunks. In fact, peaks in the number of skunk pelts sold occurred in a winter (1970-1971) between the 1969 and 1972 upsurges and the winter (1972-1973) immediately following the 1972 outbreak.

A gradual decline in the number of skunks collected by trappers in northeastern Tennessee prior to the increase in skunk rabies cases was similar to data for the entire state (Fig. 23). There was a precipitous decline in the number of striped skunk pelts sold by all Tennessee trappers during the 1950's (Warren 1975:46). In the season designated as 1953 over 24,000 striped skunk pelts were purchased by fur buyers in Tennessee, but by 1958 the number had declined to less than 2,000 and generally remained below 3,000 pelts per year into the early 1970's. In an analysis of this trend Warren (1975:26) stated that there "is no correlation between the numbers of pelts marketed and pelt price. Skunk populations appear to be declining." Reported skunk rabies cases first appeared in Tennessee during 1950 and continued to occur at low but persistent levels in the state during the 1950's and early 1960's. The rise of skunk rabies cases in Tennessee began in the early 1960's and major outbreaks occurred in 1965 and 1972. However, these distinct fluctuations of reported rabies among skunks were not associated with any noticeable fluctuations in the numbers of skunk pelts sold by Tennessee fur trappers.

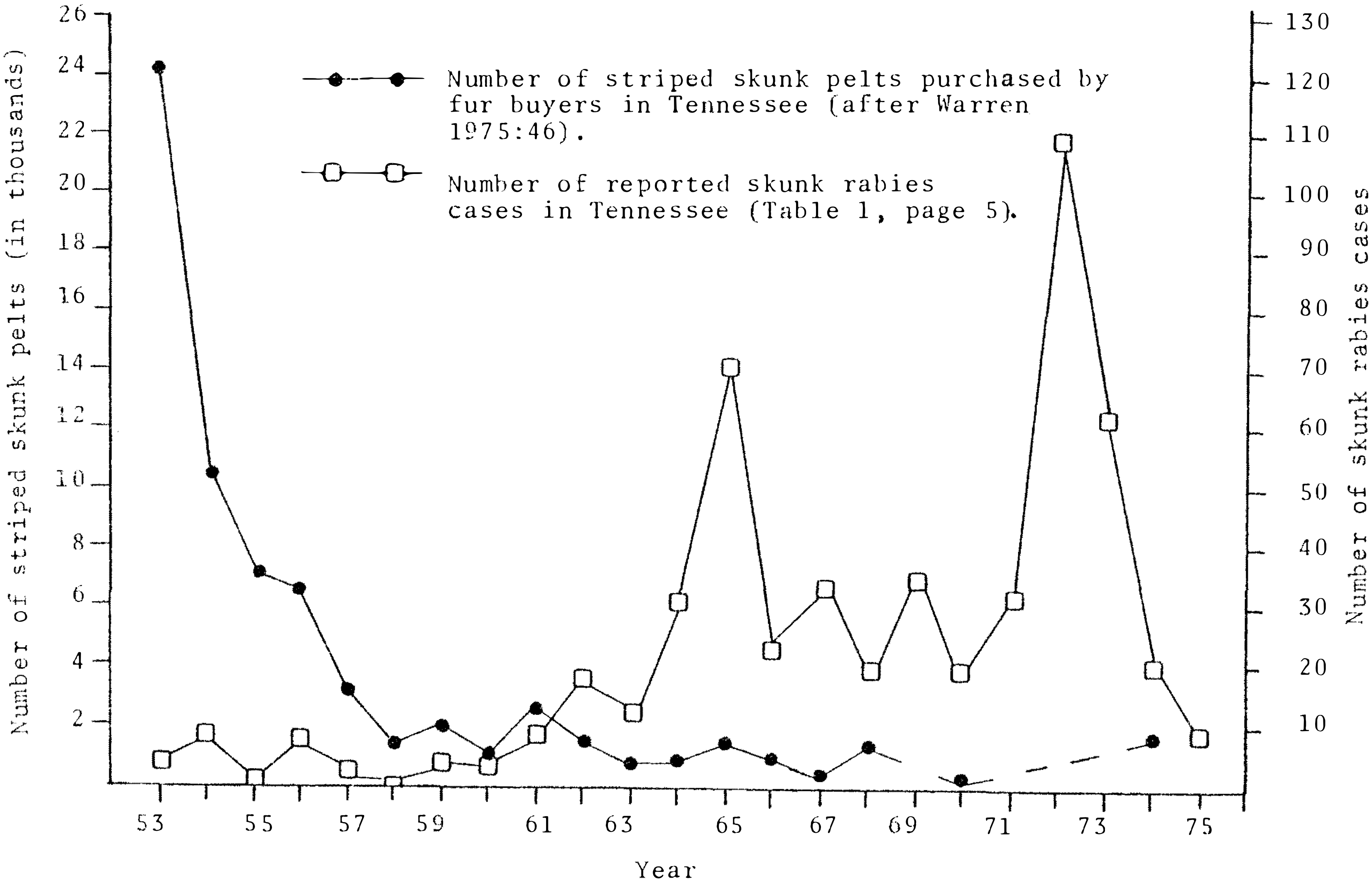


Fig. 23. Relationship between the number of striped skunk pelts purchased by fur buyers in Tennessee and the level of reported skunk rabies cases in the state, 1953-1975.

IV. RABIES CASES IN RELATION TO MAJOR ENVIRONMENTAL FEATURES

Several environmental features were considered relevant to the distribution pattern of reported rabies cases and the striped skunks which were not associated with reported skunk rabies cases. These features were the general topography, amount of forest/woodland cover, and the presence of human population centers, caves, and lakes and rivers. The data regarding these features among the 48 trap areas are summarized in Table 28.

Each trap area was assigned to one of two topographical categories based on elevation data given on U.S. Geological Survey maps. No trap area was considered to be totally within the mountainous portion of the study area, but the 18 trap areas which did contain elevations in excess of 600 m, an arbitrarily chosen figure, were designated as having a mountain/valley topography. The remaining 30 trap areas were considered to have a valley topography.

There are 19 recognized cases in 12 trap areas of the study area (Fig. 24), and probably others which have not yet been formally recorded. A brief description is given for 18 of these 19 caves by either Barr (1961) or Matthews (1971), and these descriptions mention neither the presence of bats nor indications of bat habitation. Many of these caves are either wet and muddy or contain active streams, and Mahon

Table 28. Major environmental features of the 48 trap areas.

Trap area	Human population center(s)	Recognized cave(s)	Lake or river	Approximate range in elevation (m)	Forest/woodland cover index (0-4)	Topographic designation
1	None	None	Yes	270- 460	0.89	Valley
2	Yes	Yes (1)	Yes	300- 460	0.58	Valley
3	None	None	None	350- 460	1.09	Valley
4	None	None	Yes	300- 480	0.70	Valley
5	None	None	Yes	340- 400	1.26	Valley
6	None	None	Yes	270- 430	1.44	Valley
7	None	Yes (1)	None	300- 490	1.58	Valley
8	None	None	None	330- 490	1.42	Valley
9	None	None	Yes	300- 480	0.87	Valley
10	None	Yes (2)	Yes	300- 380	1.68	Valley
11	None	None	Yes	300- 420	1.88	Valley
12	None	Yes (1)	None	330- 440	2.12	Valley
13	None	Yes (1)	Yes	300- 400	1.38	Valley
14	None	None	Yes	270- 390	1.97	Valley
15	None	None	Yes	335- 730	2.42	Mtn/Valley
16	Yes	Yes (2)	Yes	310- 730	1.34	Mtn/Valley
17	None	Yes (1)	Yes	330- 730	1.45	Mtn/Valley
18	None	None	Yes	430- 850	2.43	Mtn/Valley
19	None	None	None	360-1,040	3.02	Mtn/Valley
20	None	None	Yes	340- 980	1.62	Mtn/Valley
21	None	None	Yes	360- 950	3.69	Mtn/Valley
22	None	None	Yes	360- 850	3.07	Mtn/Valley
23	None	None	Yes	360- 790	2.95	Mtn/Valley
24	None	None	Yes	400- 980	3.88	Mtn/Valley

Table 28. continued.

Trap area	Human population center(s)	Recognized cave(s)	Lake or river	Approximate range in elevation (m)	Forest/woodland cover index (0-4)	Topographic designation
25	None	None	Yes	430- 880	3.26	Mtn/Valley
26	None	None	None	430- 850	3.73	Mtn/Valley
27	None	None	Yes	370- 460	1.11	Valley
28	None	Yes (1)	Yes	370- 490	0.68	Valley
29	None	None	Yes	400-1,160	1.95	Mtn/Valley
30	None	None	Yes	330- 400	1.92	Valley
31	None	Yes (4)	Yes	330- 430	1.53	Valley
32	None	Yes (1)	None	400- 460	0.52	Valley
33	Yes	None	Yes	400- 490	0.73	Valley
34	None	None	Yes	400- 550	1.44	Valley
35	None	None	None	460-1,220	3.25	Mtn/Valley
36	None	None	Yes	320- 430	0.68	Valley
37	None	None	None	330- 400	0.55	Valley
38	None	Yes (1)	None	370- 460	0.78	Valley
39	Yes	Yes (1)	None	400- 490	0.68	Valley
40	None	None	Yes	400- 490	0.49	Valley
41	None	None	None	330- 490	0.84	Valley
42	None	None	None	330- 400	0.63	Valley
43	None	None	None	430- 550	1.40	Valley
44	None	None	None	430- 580	0.50	Valley
45	None	None	None	350- 640	1.83	Mtn/Valley
46	None	None	None	360- 640	1.48	Mtn/Valley
47	None	Yes (2)	None	400- 610	0.92	Mtn/Valley
48	None	None	None	400- 760	1.65	Mtn/Valley

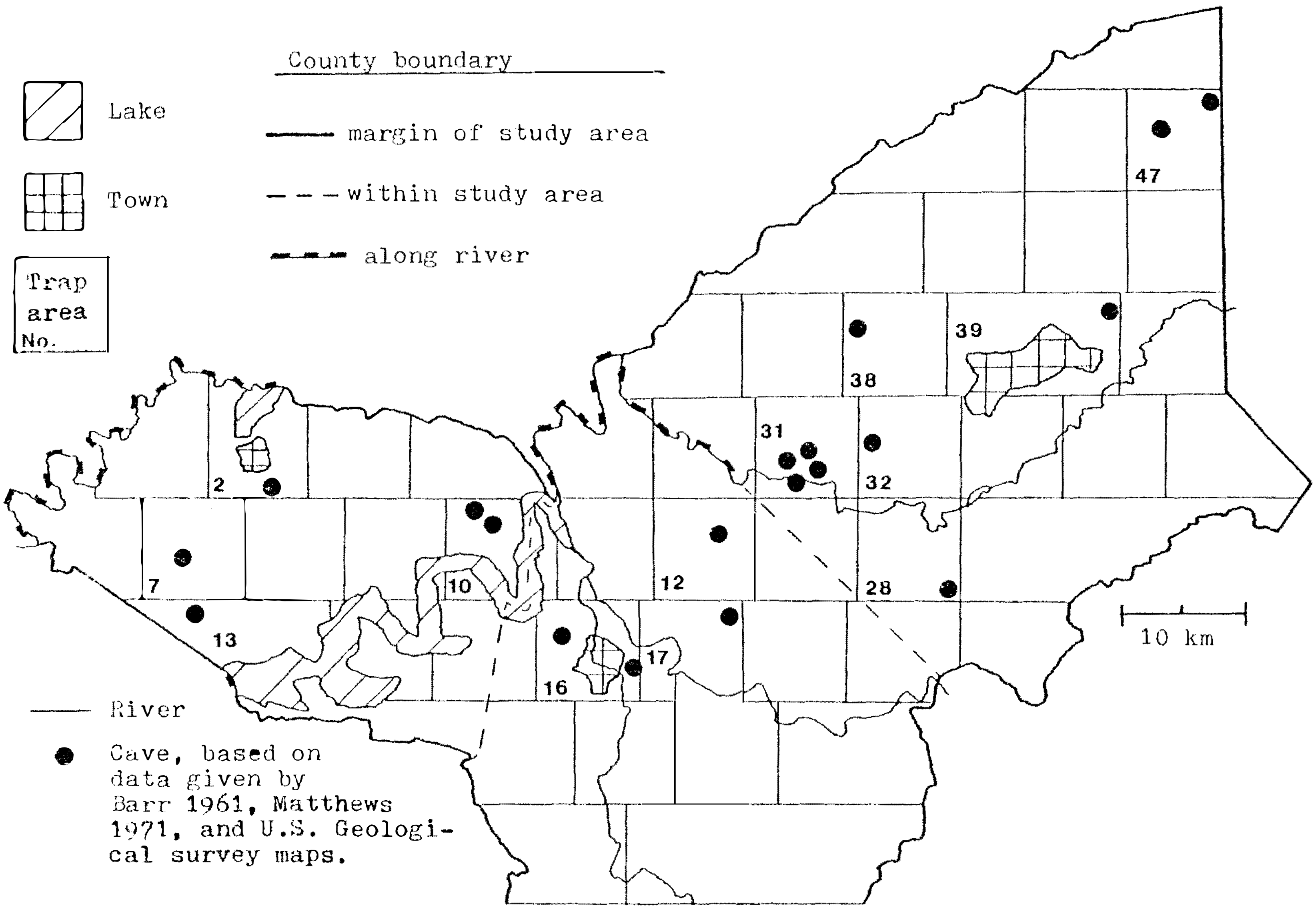


Fig. 24. Location of 19 recognized caves in the study area.

(1973:67) noted that over 90 percent of the caves containing bats in his Tennessee study were either wet or contained active streams.

Thirty-one of the 48 trap areas were considered to contain significant contact with lakes and/or rivers. However, all trap areas contain small streams and numerous farm ponds.

Only four trap areas were considered to contain significant concentrations of human population. Several other trap areas have smaller communities which serve as centers of commerce, but many people working in these small towns live in rural areas away from the concentration of commercial buildings.

The amount of forest/woodland cover is expressed by an index which ranged from 0 for areas with the least amount of cover to four for areas with the most forest/woodland cover. Using this system the values among the trap areas ranged from a low of 0.49 in trap area 40 to a high of 3.88 in trap area 24. Trap area 24 is north of and adjacent to the Great Smoky Mountains National Park.

The data from the study suggest that reported rabies cases, and perhaps actual rabies cases, did not occur randomly within the study area over the 1972-1976 period. In fact, reported rabies cases appeared to be clustered in several foci of different geographical size. Some of the 17 striped skunks which were not associated with reported skunk rabies cases (Fig. 21, page 121) were located in trap areas which did not contain any reported rabies cases (Table 20, page 97). The goal of landscape epizootiology is to establish whether any environmental disease determinants influence the occurrence of disease. Since the distribution of reported skunk rabies cases did not encompass all the trap areas with evidence of striped skunk inhabitation, one approach to this aspect of disease ecology is to establish whether any environmental differences existed between the trap areas with reported rabies cases and the trap areas containing striped skunks not associated with reported skunk rabies cases.

The point correlation coefficient (Fig. 8, page 51) was employed to indicate whether the trap areas with reported rabies cases were environmentally different from the trap areas containing striped skunks not associated with reported skunk rabies cases. Reported rabies cases among all species were used in this analysis because clinical rabies among the two cows, a horse, and a dog may have resulted from infection by a rabid skunk. Clinical rabies in the gray fox could have occurred independently of rabies in skunks.

In regard to human population centers and the 19 recognized caves in the study area, the analysis revealed almost no difference in the degree of geographical association among reported rabies cases and the striped skunks not associated with reported skunk rabies cases (Table 29).

Table 29. The degree of geographical association between trap areas with reported rabies cases (all species), trap areas with striped skunks not associated with reported skunk rabies cases (NAWRSRC), and trap areas with selected environmental features.[a]

Feature	Number of trap areas	Trap areas with reported rabies cases 1972[b] 8	1973 2	1974 4	1976 8	1976[c] (A) 15	Trap areas w/striped skunks NAWRSRC (B) 15	Difference A - B
Human population center	4	+0.067	+0.314	-0.091	-0.135	+0.128	+0.122	+0.006
Recognized caves	13	-0.147	+0.108	-0.184	-0.142	-0.011	-0.006	-0.005
Lakes/rivers	29	-0.324	+0.169	-0.064	-0.324	-0.373	+0.067	-0.306
Valley topography	30	+0.231	+0.162	+0.078	0	+0.151	+0.244	-0.093
Mountain/valley topography	18	-0.213	-0.162	-0.078	0	-0.151	-0.244	+0.093

[a]Geographical association is expressed by the point correlation coefficient.

[b]Based on the location of 75 percent (18/24) of the reported rabies cases during 1972.

[c]The single horse rabies case in 1975 is not considered as a separate year but is included in the total.

In regard to topography the analysis showed that both groups of animals had positive associations with valley topography, and again the coefficients of association were similar. The most noticeable difference was with respect to lakes and rivers. During the 1972-1976 period reported rabies cases had a negative statistical association (-0.373) with those trap areas containing major lakes and/or rivers while the striped skunks not associated with reported skunk rabies cases showed a slightly positive statistical association (+0.067) with these trap areas. Some reported rabies cases did occur near rivers and lakes, particularly in trap areas 1, 2, 34, and 40. However, the concentration of reported rabies cases in northern Greene County was some distance from a major lake or river.

While the negative association between caves and reported rabies cases is not large (-0.011), caves are more abundant in the central part of the study area and most of the reported rabies cases occurred in the northeastern and northwestern parts of the three-county area. This lack of geographical overlap in the distribution of caves and reported rabies cases does not support the idea that terrestrial wildlife are infected with rabies through contact with rabid cave-dwelling bats. The role of bats as a possible source of the rabies virus for terrestrial wildlife in the study area could not be ascertained, but bats are present in the study area and they may use abandoned buildings or trees rather than caves as roosting sites.

Both reported rabies cases and the striped skunks not associated with reported rabies cases showed a degree of positive statistical association with the four trap areas considered as centers of human population. The indication that reported rabies cases were not strongly associated with these areas of high human population density suggests that the reporting of rabies cases may not be completely dependent on large numbers of human observers. Based on observations during the trap effort, the human population density within the study area did not vary sufficiently to account for the noticeable concentrations of reported rabies cases in eastern Greene County and northwestern Jefferson County or the total lack of reported rabies cases in Cocke County and western Greene County.

The analysis with respect to the amount of forest/woodland cover, the only environmental factor which varied over a quantitative spectrum rather than a present or absent designation, was slightly different. The 46 reported rabies cases with documented locations were divided into two groups, early rabies cases and late rabies cases (Fig. 25). Those cases reported from January through March were designated as early rabies cases. There were 20 early rabies cases during the 1972-1976 period, all of which occurred among striped skunks in nine trap areas. The 26 rabies cases reported from April through December were designated as late

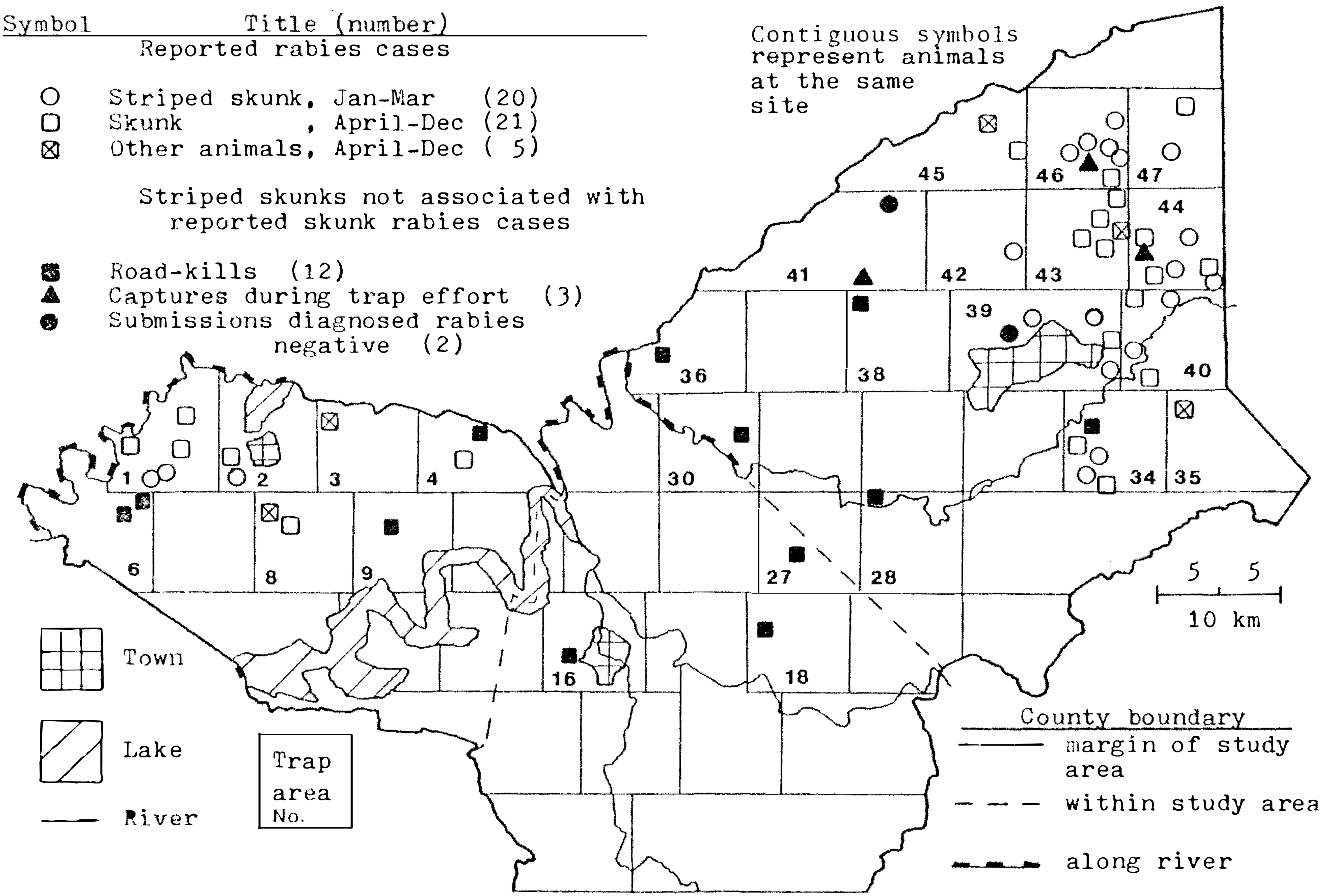


Fig. 25. Distribution of reported rabies cases (all species, 1972-1976) and striped skunks not associated with reported skunk rabies cases, 1972-1976.

rabies cases. These late rabies cases included 21 skunks, two cows, a horse, a dog, and a gray fox. Six of the 15 trap areas containing reported rabies cases were involved with late rabies cases only.

The 48 trap areas were ranked by the amount of forest/woodland cover as expressed by the established index and divided into eight groups of six trap areas each. Data regarding the occurrence of reported rabies cases and striped skunks not associated with reported skunk rabies cases among these six groups of trap areas are given in Table 30.

The largest number of reported rabies cases occurred in the group of trap areas with the least amount of forest/woodland cover, Group 1. The Spearman rank correlation coefficient between the degree of forest/woodland cover and the number of reported rabies cases was -0.67 which represents a significant inverse association ($P < .025$).

The point correlation coefficients between each group of trap areas ranked by cover indices and the trap areas with some early rabies cases, only late rabies cases, all rabies cases, and striped skunks not associated with reported skunk rabies cases are given in Table 31. The early rabies cases had the largest positive statistical association with the trap areas containing the least forest/woodland cover. The trap areas with only late rabies cases were predominantly the ones with medium forest/woodland cover, Group 4 areas.

Table 30. The 48 trap areas ranked by amount of forest/woodland cover (expressed by the cover index) with the number of reported rabies cases (all species, 1972-1976) and the number of striped skunks not associated with reported skunk rabies cases (NAWRSRC).

Trap area	Forest/ woodland cover index	Reported rabies cases 1972-1976		Striped skunks NAWRSRC			Data for 6 trap area group		
		Early[a]	Late[b]	Road-kills	Captures	Diagnosed negative	Average cover index	Rabies cases	Striped skunks NAWRSRC
40	0.490	2	2	-	-	-			
44	0.500	3	3	-	1	-	Group 1 (least forest/woodland cover)		
32	0.515	-	-	-	-	-			
37	0.550	-	-	-	-	-			
2	0.585	1	1	-	-	-	0.545	13	1
42	0.630	1	-	-	-	-			
36	0.678	-	-	1	-	-			
39	0.680	3	1	-	-	1			
28	0.684	-	-	1	-	-	Group 2		
4	0.697	-	1	1	-	-			
33	0.727	-	-	-	-	-	0.708	5	5
38	0.780	-	-	1	-	-			
41	0.839	-	-	-	1	1			
9	0.874	-	-	1	-	-			
1	0.893	2	3	-	-	-	Group 3		
47	0.922	1	1	-	-	-			
3	1.090	-	1	-	-	-	0.955	8	4
27	1.112	-	-	1	-	-			
5	1.261	-	-	-	-	-			
16	1.340	-	-	1	-	-			
13	1.385	-	-	-	-	-	Group 4		
43	1.400	-	5	-	-	-			
8	1.416	-	2	-	-	-	1.374	11	2
34	1.440	3	1	1	-	-			

Table 30. continued.

Trap area	Forest/ woodland cover index	Reported rabies cases 1972-1976 Early[a]	Late[b]	Striped skunks NAWRSRC Road-kills	Captures	Diagnosed negative	Data for 6 trap area group Average cover index	Rabies cases	Striped skunks NAWRSRC
6	1.442	-	-	2	-	-			
17	1.446	-	-	-	-	-		Group 5	
46	1.485	6	-	-	1	-			
31	1.527	-	-	-	-	-	1.517	6	3
7	1.581	-	-	-	-	-			
20	1.622	-	-	-	-	-			
48	1.652	-	-	-	-	-			
10	1.685	-	-	-	-	-		Group 6	
45	1.833	-	2	-	-	-			
11	1.885	-	-	-	-	-	1.820	2	1
30	1.917	-	-	1	-	-			
29	1.948	-	-	-	-	-			
14	1.968	-	-	-	-	-			
12	2.120	-	-	-	-	-		Group 7	
15	2.416	-	-	-	-	-			
18	2.433	-	-	1	-	-	2.486	0	1
23	2.954	-	-	-	-	-			
19	3.023	-	-	-	-	-			
22	3.073	-	-	-	-	-			
35	3.253	-	1	-	-	-		Group 8	
25	3.259	-	-	-	-	-		(most forest/woodland cover)	
21	3.686	-	-	-	-	-			
26	3.733	-	-	-	-	-	3.480	1	0
24	3.876	-	-	-	-	-			

[a]Cases reported during January-March period.

[b]Cases reported during April-December period.

Table 31. The degree of geographical association between the amount of forest/woodland cover in groups of six trap areas and trap areas with some early rabies cases, late rabies cases only, all reported rabies cases, and striped skunks not associated with reported skunk rabies cases (NAWRSRC).[a]

Groups of 6 trap areas ranked by cover index	Number of trap areas	Some in Jan.-Mar. (early)	All in Apr.-Dec. (late)	Total A	Striped skunks NAWRSRC B	Difference A - B
		Number of trap areas				
		9	6	15	15	
Group 1	6	+0.464	-0.143	+0.289	-0.119	+0.408
Group 2	6	-0.020	+0.047	+0.017	+0.425	-0.408
Group 3	6	+0.141	+0.047	+0.153	+0.153	0
Group 4	6	-0.020	+0.238	+0.153	+0.017	+0.136
Group 5	6	-0.020	-0.143	-0.119	+0.017	-0.136
Group 6	6	-0.182	+0.047	-0.119	-0.119	0
Group 7	6	-0.182	-0.143	-0.255	-0.119	-0.136
Group 8	6	-0.182	+0.047	-0.119	-0.255	+0.136
Total (Statistical check)		-0.001	-0.003	0.000	0.000	0.000

[a]Association is expressed by the point correlation coefficient which ranges from +1 for totally identical patterns to -1 for total dissimilarity.

The only reported rabies case in any of the 21 trap areas with the highest indices of forest/woodland cover occurred after mid-April. The 17 striped skunks which were not associated with reported rabies cases showed the highest positive statistical association with the 12 trap areas in Groups 2 and 3, areas with low to moderate forest/woodland cover and between the group of areas with numerous early rabies cases and the group of areas with numerous late rabies cases. The associations among these three groups of animals and the ranked groups of trap areas are shown graphically in Fig. 26.

These data in Table 31 and Fig. 26 suggest that rabid animals in the study area were reported primarily in trap areas with slightly less cover (early rabies cases) or slightly more cover (late rabies cases) than the trap areas which contained striped skunks not associated with reported skunk rabies cases. These three groups of animals had negative or low positive statistical associations with those trap areas having relatively large amounts of forest/woodland cover.

V. THE SERUM SURVEY AND ANALYSIS OF SALIVARY GLANDS

Serum Survey, 1973

During 1973 trapping was conducted from May through early October. This trap effort employed 2,235 trap nights

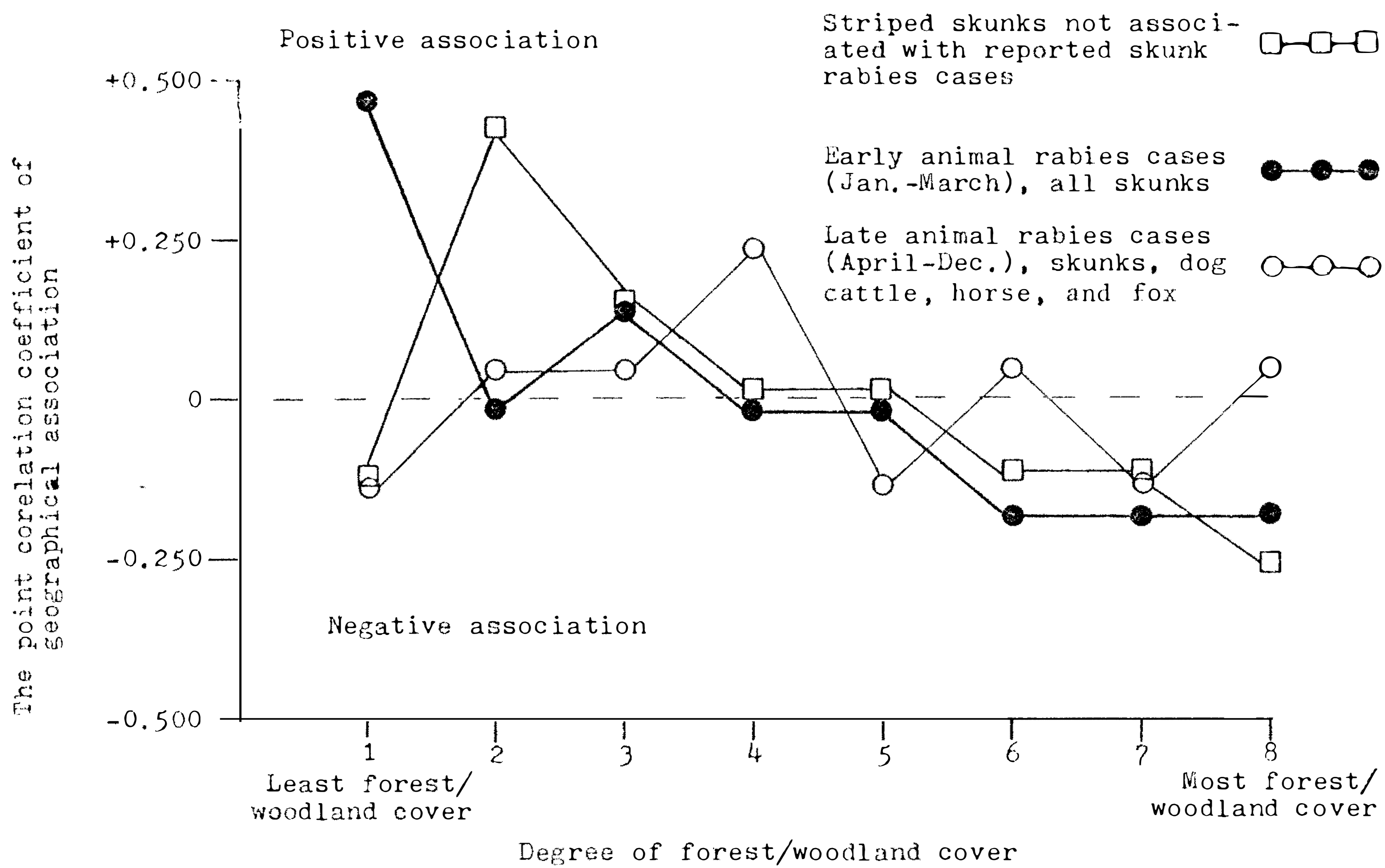


Fig. 26. The degree of association between groups of six trap areas with varying degrees of forest/woodland cover and trap areas with some early rabies cases, only late rabies cases, and striped skunks not associated with reported skunk rabies cases. Data from Table 31.

at 794 sites. From the 170 opossums captured, 65 opossum serum samples were tested for the presence of rabies antibodies. The difference between the number of opossums captured and the number used in the serum survey was the result of (1) the exclusion of opossums during the early part of the study in an effort to concentrate on striped skunks and (2) serum samples which were inadequate for analysis. The latter situation occurred primarily when only small blood samples were collected in the field, usually from very young opossums. The 65 samples tested for antibodies were collected during the August-October period.

The serum analyses performed at CDC revealed that one opossum (1.5 percent) was definitive rabies seropositive (DRSP), nine opossums (13.8 percent) were presumptive rabies seropositive (PRSP), and 55 (84.6 percent) were rabies seronegative (RSN) (Table 32). The nine PRSP opossums had RFFIT titers which ranged from 1:5, the minimum seropositive titer for this study, to 1:70. The single DRSP opossum had a RFFIT titer of 1:56 and a serum neutralization (SN) titer of 1:2, the only dilution tested.

Females comprised 65 percent (42/65) of the opossums sampled, and all 10 seropositive opossums were females. The presence of seropositive animals among females was significantly higher ($P < .05$) than among males. For statistical analysis juveniles and subadults were combined into a nonadult category. While most seropositive opossums (8/10) were

Table 32. Results of the 1973 serum survey among opossums by sex and weight class.

Age	Juvenile				Subadult		Adult								Total		
	Weight classes are defined in Table 24, page 107																
Wt.	1		2		3		4		5		6		7				
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
Sample	1	6	5	1	6	9	6	12	3	11	1	3	1	0	23	42	65
% Total	2	9	8	2	9	14	9	18	5	17	2	5	2	-	35	65	
Presumptive rabies seropositive (PRSP)																	
Number	0	0	0	0	0	2	0	2	0	4	0	1	0	-	0	9	9
% Sample	-	-	-	-	-	22	-	17	-	36	-	33	-	-	-	21	14
% Weight class	-		-		13		11		29		25		-				
Definitive rabies seropositve (DRSP)																	
Number	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1
% Sample	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	2	2
% Weight class	-		-		-		6		-		-		-				
All rabies seropositive, by weight class																	
Number	0		0		2		3		4		1		0		0	10	10
% Weight class	-		-		13		17		29		25		-		-	24	15

adults, the proportion was not significantly different from nonadults ($P > .10$). Detailed data on the 1973 serum survey by sex, weight class, and trap area are given in Appendix M.

The capture sites of the 65 opossums tested during 1973 are shown in Fig. 27. At least one serum sample was tested from 25 of the 48 trap areas, and seropositive opossums were found in seven trap areas. Some of the seropositive opossums were captured at sites near the locations of reported rabies cases of past, present, or future years (Table 33). In trap area 1, two of the four opossums tested were rabies seropositive. Both of these opossums were collected during August, and were located within 8 km of the nine rabid striped skunks reported in trap areas 1 and 2 during the 1973-1974 period. The PRSP opossum captured in trap area 8 was 3.5 km from the site of the rabid cow reported during September 1972 and less than 1.6 km from the site of the rabid striped skunk reported during June 1974.

There was a cluster of four PRSP opossums in trap areas 45 and 46. Three of the four opossums collected in trap area 46 were rabies seropositive, and the single RSN opossum was a 250 g male captured in mid-September. Two of the three seropositive opossums were adults, and the third was a 1.0 kg female. Since Greene County was free of reported rabies cases during 1973, this PRSP subadult female, probably born in early 1973, was apparently exposed to rabies in the absence of reported, but not necessarily actual,

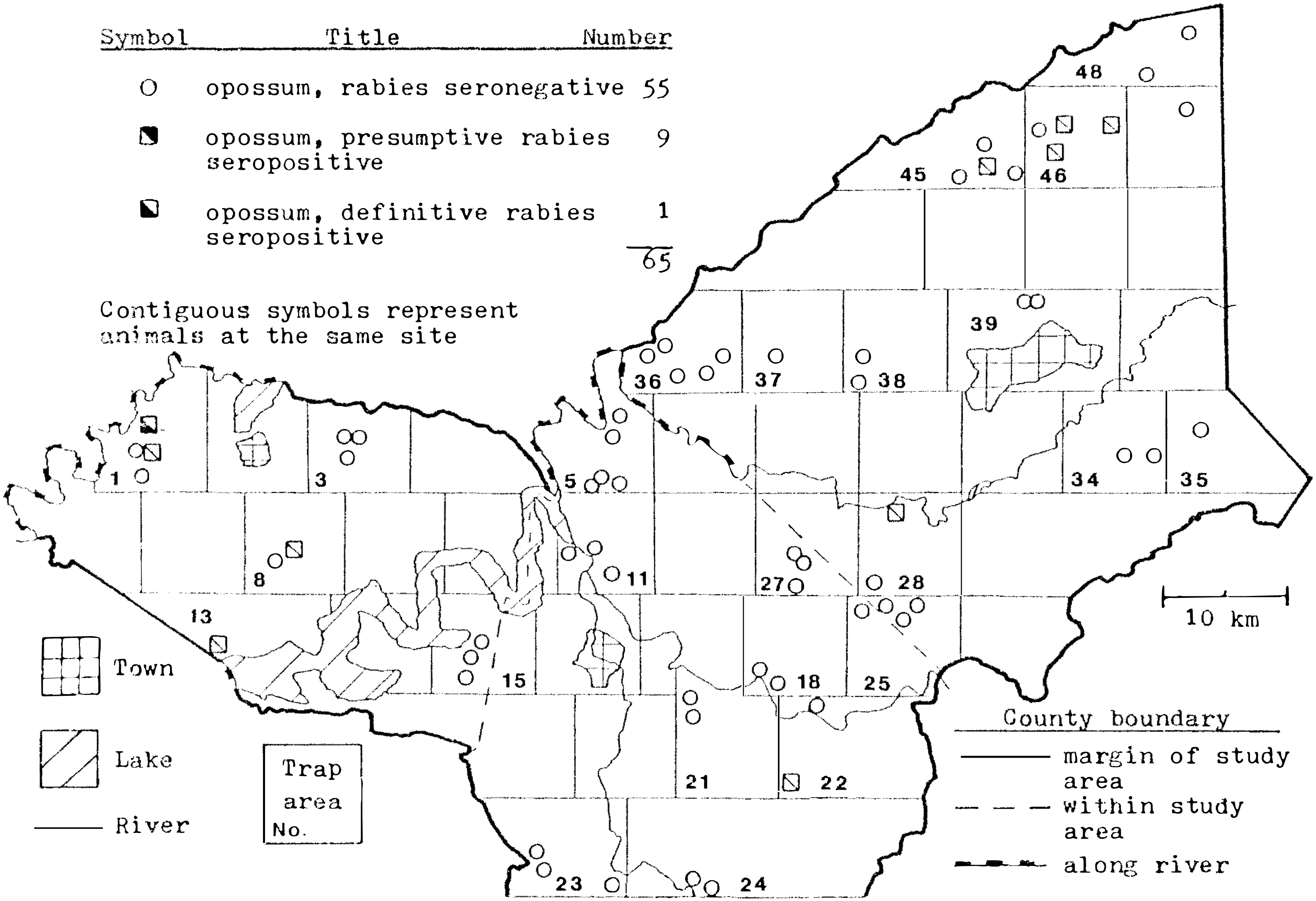


Fig. 27. Location of the 65 opossums tested for rabies antibodies in the study area, 1973.

Table 33. Results of the 1973 serum survey among opossums by trap area in relation to reported rabies cases during the 1972-1974 period.

Trap area	Number of opossums Tested	PRSP	DRSP	All seropositives Number	Percent	Reported rabies cases 1972	1973	1974
1	4	1	1	2	50	0	3	2
3	3	0	0	0	0	0	0	0
5	5	0	0	0	0	0	0	0
8	2	1	0	1	50	1	0	1
11	3	0	0	0	0	0	0	0
13	1	1	0	1	100	0	0	0
15	3	0	0	0	0	0	0	0
18	2	0	0	0	0	0	0	0
21	2	0	0	0	0	0	0	0
22	2	1	0	1	50	0	0	0
23	3	0	0	0	0	0	0	0
24	2	0	0	0	0	0	0	0
25	4	0	0	0	0	0	0	0
27	3	0	0	0	0	0	0	0
28	2	1	0	1	50	0	0	0
34	2	0	0	0	0	3	0	0
35	1	0	0	0	0	0	0	0
36	5	0	0	0	0	0	0	0
37	1	0	0	0	0	0	0	0
38	2	0	0	0	0	0	0	0
39	2	0	0	0	0	4	0	0
45	4	1	0	1	25	0	0	1
46	4	3	0	3	75	4	0	0
47	1	0	0	0	0	0	0	0
48	2	0	0	0	0	0	0	0
Total	65	9	1	10	15	12[a]	3[b]	4[c]

[a]There were 24 reported rabies cases in the study area during 1972 with other documented cases in trap area (TA) 40 (2 cases), TA 42 (1 case), TA 43 (1 case), and TA 44 (2 cases).

[b]Two other reported cases occurred in TA 2.

[c]One other reported case occurred in TA 4.

clinical rabies cases in the area. However, there were four rabid skunks reported in trap area 46 during the first three months of 1972, and these cases included the first two cases (72-1 and 72-2) reported in the county for that year. Within trap area 46 the locations of rabies seropositive opossums during 1973 and rabid skunks from 1972 were separated by as little as 1 km. In trap area 45, the three RSN opossums were all juveniles, and the only adult sampled was PRSP. This PRSP opossum was approximately 2 km from the site of the rabid striped skunk reported during May 1974, the only reported rabies case in Greene County during 1974.

In considering the reported rabies cases in Greene County, trap areas 45 and 46 were found to be special. The single reported rabies case during both 1974 and 1975 occurred in trap area 45, and some of the earliest reported rabies cases during 1972 and 1976 occurred in trap area 46. It is interesting to note, therefore, that rabies seropositive opossums were apparently clustered in the same areas of Greene County where these early or only reported rabies cases were found over several years.

During 1973 PRSP opossums also occurred in three trap areas (13, 22, and 28) which were not associated with reported rabies cases during any year of the study.

Serum Survey, 1974

During 1974 trapping was conducted from February to early June. This trap effort employed 2,161 trap nights at 744 sites. Two striped skunks and 195 opossums were captured, and serum analyses were performed for 192 opossums and both striped skunks.

The two striped skunks were both adult males. The skunk captured in trap area 46 was DRSP, and the skunk sampled in trap area 41 was rabies seronegative. Among the 192 opossums, 12 (6.2 percent) were DRSP, 31 (16.1 percent) were PRSP, and 149 (77.6 percent) were RSN (Table 34). Detailed data on the 1974 serum survey among opossums by sex, weight class, and trap area are given in Appendix N.

Sixty-one percent (118/192) of the opossums tested were females. There was a smaller percentage of PRSP females, 13.6 percent against 20.3 percent among males, but a greater percentage of females were DRSP, 6.8 percent against 5.4 percent among males. These differences were not significant ($P > .05$). The statistical comparison among age classes was again based on nonadults and adults. While only two percent (1/43) of the seropositive opossums occurred among the 10 percent (20/192) of the sample considered to be nonadults, the seropositive animals within the two age categories were not significantly different ($P > .05$).

From trap areas 1-24 opossums were sampled by roadside trapping in 23 areas and from two farms located in trap area 1

Table 34. Results of the 1974 serum survey among opossums by sex and weight classes.

Age	Juvenile				Subadult		Adult										
	Weight classes are defined in Table 24, page 107																
Wt.	1		2		3		4		5		6		7		Total		
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
Sample	7	7	1	3	0	2	4	49	19	35	33	16	10	6	74	118	192
% Total	4	4	1	2	-	1	2	26	10	18	17	8	5	3	38	61	
Presumptive rabies seropositive (PRSP)																	
Number	1	0	0	0	-	0	0	7	4	8	8	0	2	1	15	16	31
% Sample	14	-	-	-	-	-	-	14	21	23	24	-	20	17	20	14	16
% Weight class	7		-		-		13		22		16		19				
Definitive rabies seropositive (DRSP)																	
Number	0	0	0	0	-	0	0	5	1	2	2	1	1	0	4	8	12
% Sample	-	-	-	-	-	-	-	10	5	6	6	6	10	-	5	7	6
% Weight class	-		-		-		9		6		6		6				
All rabies seropositive, by weight class																	
Number	1		0		0		12		15		11		4		19	24	43
% Weight class	7		-		-		23		28		22		25		26	20	22

(Table 35). Seropositive opossums collected by roadside trapping were found in 11 trap areas, and the percentage of seropositive opossums ranged from 25 to 67. Seropositive opossums appeared to be very prevalent on the two farms where rabid striped skunks had occurred; 50 and 80 percent of the opossums on these two farms were found to be rabies seropositive. The capture sites of the 105 opossums tested from trap areas 1-24 are shown in Fig. 28.

The data from roadside and farm trapping in trap area 1 were interesting in that 62 percent (8/13) of the opossums collected in farm trapping were rabies seropositive, and yet none of the 12 opossums collected in roadside trapping, the largest sample from any trap area during 1974, had rabies antibodies. Therefore, both farms on which rabid skunks were found appeared to represent compact foci of rabies seropositive opossums.

Among the other 22 trap areas sampled seropositive opossums were found in 10 trap areas. During the three-year period (1973-1975) which bracketed the 1974 serum survey, rabid animals were reported in three of these 22 areas (trap areas 2, 4, and 8). The three opossums sampled in trap area 8 were all rabies seronegative. Two of the six opossums collected in trap area 4 were PRSP. These two PRSP opossums were separated from the site of the rabid striped skunk by 3.5 km and 400 m. The single PRSP opossum in trap area 3 was approximately 6.5 km from the site of the rabid skunk in

Table 35. Results of the 1974 serum survey among opossums in trap areas 1-24 in relation to reported rabies cases among all species during the 1973-1975 period.

Trap area	Number of opossums: Tested	PRSP	DRSP	All seropositives: Number	All seropositives: Percent	Reported rabies cases: 1973	1974	1975
1	12	0	0	0	0	3	a	0
Farm C	8	3	1	4	50	-	1	-
Farm K	5	3	1	4	80	-	1	-
2	3	0	2	2	67	2	0	0
3	3	1	0	1	33	0	0	0
4	6	2	0	2	33	0	1	0
5	5	2	0	2	40	0	0	0
6	4	1	0	1	25	0	0	0
7	4	0	0	0	0	0	0	0
8	3	0	0	0	0	0	1	0
9	5	0	0	0	0	0	0	0
10	7	0	2	2	29	0	0	0
11	8	1	2	3	38	0	0	0
12	3	0	0	0	0	0	0	0
13	2	0	0	0	0	0	0	0
14	2	0	0	0	0	0	0	0
15	2	1	0	1	50	0	0	0
16	2	1	0	1	50	0	0	0
17	3	0	0	0	0	0	0	0
18	3	0	0	0	0	0	0	0
19	6	0	0	0	0	0	0	0
20	3	1	0	0	33	0	0	0
22	2	0	0	0	0	0	0	0
23	3	1	0	1	33	0	0	0
24	1	0	0	0	0	0	0	0
Total	105	17	8	25	24	5	4	0

[a]Two rabid striped skunks occurred in trap area 1 during 1974, but these animals are considered as occurring on the farms which were located in trap area 1.

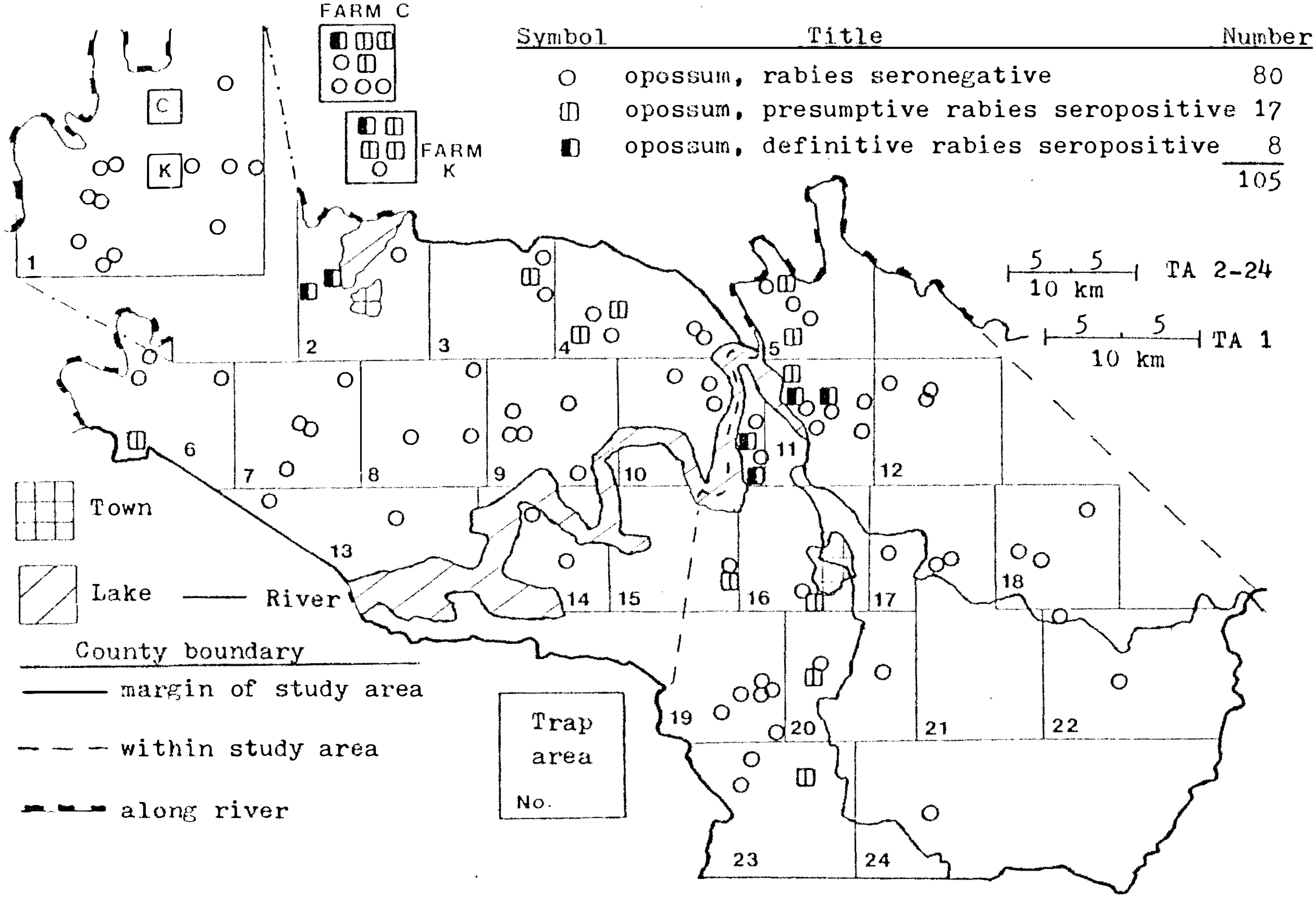


Fig. 28. Location of the 105 opossums tested for rabies antibodies in trap areas 1-24, 1974. Contiguous symbols represent animals at the same site.

trap area 4. The highest percentage of seropositive opossums in any trap area was 67 percent which occurred in trap area 2 where two rabid striped skunks were reported during 1973. The two DRSP opossums in trap area 2 were both within 5 km of the two rabid skunks of 1973 and within 6.5 km of the two rabid skunks which were reported from trap area 1 during 1974.

Twelve rabies seropositive opossums appeared isolated from reported rabies cases in the Jefferson-Cocke County area during the 1973-1975 period. The four DRSP opossums in trap area 10 (29 percent seropositive opossums) and trap area 11 (38 percent seropositive opossums) were located in a relatively small section of Cocke County. Cocke County had been free of reported rabies cases since 1967. The nearest reported rabies case to these four opossums was the rabid skunk reported during June 1974 in trap area 4 across the French Broad River. The six PRSP opossums in trap areas 5, 11, 16, 20, and 23 occurred in a pattern which suggested a positive geographical association with parts of the river system in Cocke County. Seropositive opossums appeared along the Nolichucky River in the northern part of the county (trap area 5), along the French Broad River (trap area 11), and into the southern part of the county along the Pigeon River (trap areas 16, 20, and 23). The single PRSP opossum in trap area 15 was approximately 5 km from both the Pigeon and French Broad rivers. The single PRSP opossum in trap area 6 was approximately 3.5 km from the Holston River.

Among trap areas 25-48 opossum serum samples were collected from 23 trap areas during 1974 (Table 36). A DRSP striped skunk was found in trap area 46, and a rabies seronegative striped skunk was collected in trap area 41. The overall percentage of seropositive opossums (21 percent) in trap areas 25-48 was similar to that (24 percent) found among opossums in trap areas 1-24. The capture sites for the two striped skunks and 87 opossums tested in trap areas 25-48 are shown in Fig. 29.

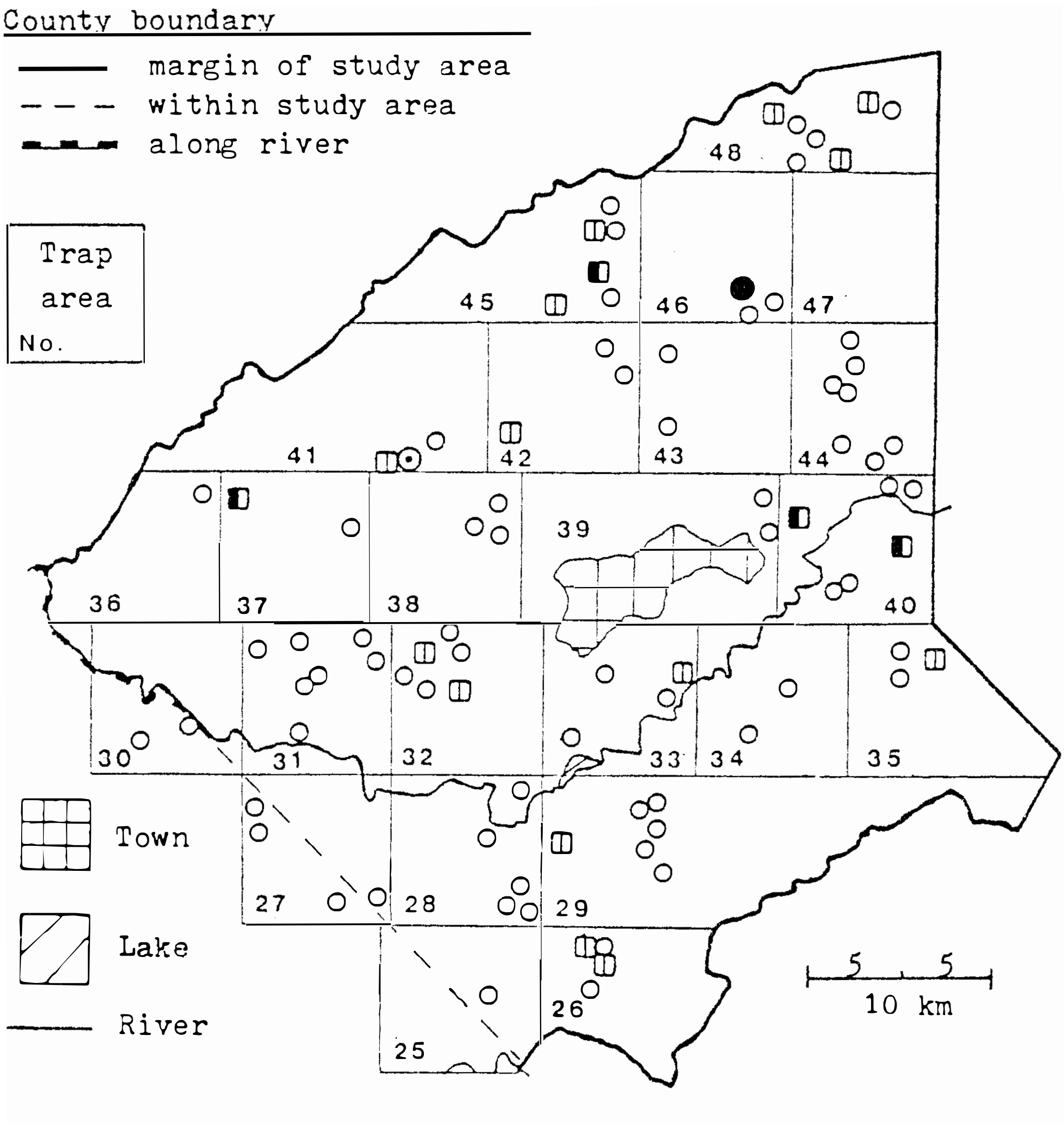
The three-year period of 1973-1975 which bracketed the 1974 serum survey represented an interepizootic period in Greene County. Only two reported rabies cases occurred during these three years, and both of these cases were found in trap area 45. Despite the low level of reported rabies cases, rabies seropositive animals (opossum or skunk) occurred in 12 trap areas during 1974.

Trap area 45 was among the four trap areas where 50 percent of the opossums tested were rabies seropositive. The DRSP opossum in this area was approximately 2 km from the rabid skunk reported during 1974, and the two PRSP opossums were both within 5 km of this rabid skunk. The DRSP striped skunk in trap area 46 was less than 5 km from the site of the rabid striped skunk in trap area 45.

In two adjacent trap areas the seropositive opossums of 1974 were not geographically associated with reported rabies cases of the 1973-1975 period, but were related to

Table 36. Results of the 1974 serum survey among opossums in trap areas 25-48 in relation to reported rabies cases among all species during the 1973-1975 period.

Trap area	Number of opossums: Tested	PRSP	DRSP	All seropositives: Number	All seropositives: Percent	Reported rabies cases: 1973	1974	1975
25	1	0	0	0	0	0	0	0
26	4	2	0	2	50	0	0	0
27	4	0	0	0	0	0	0	0
28	5	0	0	0	0	0	0	0
29	6	1	0	1	17	0	0	0
30	2	0	0	0	0	0	0	0
31	7	0	0	0	0	0	0	0
32	6	2	0	2	33	0	0	0
33	4	1	0	1	25	0	0	0
34	2	0	0	0	0	0	0	0
35	3	1	0	1	33	0	0	0
36	1	0	0	0	0	0	0	0
37	2	0	1	1	50	0	0	0
38	3	0	0	0	0	0	0	0
39	2	0	0	0	0	0	0	0
40	6	0	2	2	33	0	0	0
41	2	1	0	1	50	0	0	0
42	3	1	0	1	33	0	0	0
43	2	0	0	0	0	0	0	0
44	7	0	0	0	0	0	0	0
45	6	2	1	3	50	0	1	1
46	2	0	0	0	0	0	0	0
48	7	3	0	3	43	0	0	0
Total	87	14	4	18	21	0	1	1



Symbol	Title	Number
○	opossum, rabies seronegative	69
⊙	striped skunk, rabies seronegative	1
◫	opossum, presumptive rabies seropositive	14
◧	opossum, definitive rabies seropositive	4
●	striped skunk, definitive rabies seropositive	1
		89

Fig. 29. Location of the 87 opossums and two striped skunks tested for rabies antibodies in trap areas 25-48, 1974. Contiguous symbols represent animals at the same site.

reported cases which were to occur during 1976. There were two DRSP opossums in trap area 40 during 1974. This area contained two rabid skunks during 1972 and two rabid skunks during 1976. The PRSP opossum in trap area 35 was only 1.6 km from the site of the rabid dog, presumably infected by a rabid skunk, reported during 1976.

The 12 rabies seropositive opossums in trap areas 26, 29, 32, 33, 37, 41, 42, and 48 were set apart from the locations of most reported rabies cases. The only reported rabies case in any of these eight areas was the rabid striped skunk reported in trap area 42 during March 1972. The single PRSP opossum in trap area 41 was captured at the same site as the rabies seronegative striped skunk.

In three trap areas rabies seropositive animals were absent from sites near the locations of reported rabies cases. A total of 15 rabid animals were reported from trap areas 34, 43, and 44 during 1972 and 1976, but the 11 opossums tested from these areas during 1974 were all rabies seronegative.

Serum Survey, 1975

During 1975 trapping was conducted from May through September. This trap effort employed 1,688 trap nights at 626 sites. Ninety-four percent of the sites used during 1975 had been used in one or both of the two previous years of the study. All trapping was done at roadside sites. No skunks were captured, but 314 opossums and 117 free-roaming domestic cats were captured. Serum analyses were performed on samples from 298 opossums and 57 cats. The results of the survey among opossums will be considered first.

The serum analyses revealed that three opossums (1.0 percent) were DRSP, 41 (13.8 percent) were PRSP, and 254 (85.2 percent) were rabies seronegative (Table 37). Detailed data on the survey among opossums by sex, weight class, and trap area are given in Appendix O. Sixty-three percent (187/298) of the opossums tested were females, and 61 percent (25/41) of the PRSP opossums were females. All three DRSP opossums were adult females, but sexual differences among PRSP and DRSP opossums were not significant. While the sample sizes among the weight classes varied, statistical analysis among six groups (weight classes 1 and 2 combined) showed that seropositive opossums were not randomly distributed among the weight classes ($P < .05$). The number of seropositive opossums was higher among adults where 91 percent (40/44) of the seropositive animals were found among 74 percent (222/298) of the total sample.

During 1975 there were no reported rabies cases in trap areas 1-24 (Table 38). However, 19 percent (28/147) of the opossums in these areas were rabies seropositive, and seropositive opossums were found in 58 percent (14/24) of the trap areas. The capture sites of the 147 opossums tested in trap areas 1-24 are shown in Fig. 30.

The two DRSP opossums both had serum neutralization

Table 37. Results of the 1975 serum survey among opossums by sex and weight class.

Age	Juvenile				Subadult		Adult										
	Weight classes are defined in Table 24, page 107																
Wt.	1		2		3		4		5		6		7		Total		
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
Sample	9	5	15	7	19	21	20	33	14	76	15	37	19	8	111	187	298
% Total	3	2	5	2	6	7	7	11	5	26	5	12	6	3	37	63	
Presumptive rabies seropositive (PRSP)																	
Number	0	0	1	1	1	1	1	6	7	10	2	5	4	2	16	25	41
% Sample	-	-	7	14	5	5	5	18	50	13	13	14	21	25	14	13	14
% Weight class	-		9		5		13		19		13		22				
Definitive rabies seropositive (DRSP)																	
Number	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	3	3
% Sample	-	-	-	-	-	-	-	-	-	1	-	5	-	-	-	2	1
% Weight class	-		-		-		-		1		4		-				
All rabies seropositive, by weight class																	
Number	0		2		2		7		18		9		6		16	28	44
% Weight class	-		9		5		13		20		17		22		14	15	15

Table 38. Results of the 1975 serum survey among opossums in trap areas 1-24 in relation to reported rabies cases among all species during the 1974-1976 period.

Trap area	Number of opossums					Reported rabies cases		
	Tested	PRSP	DRSP	All seropositives Number	All seropositives Percent	1974	1975	1976
1	7	4	0	4	57	2	0	0
2	2	0	0	0	0	0	0	0
3	5	1	0	1	20	0	0	1
4	6	1	0	1	17	1	0	0
5	8	2	0	2	25	0	0	0
6	6	1	0	1	17	0	0	0
7	8	0	0	0	0	0	0	0
8	4	0	0	0	0	1	0	0
9	10	2	0	0	20	0	0	0
10	7	2	1	3	43	0	0	0
11	3	0	0	0	0	0	0	0
12	7	1	0	1	14	0	0	0
13	6	1	0	1	17	0	0	0
14	8	1	0	1	12	0	0	0
15	8	1	0	1	12	0	0	0
16	8	3	1	4	50	0	0	0
17	5	1	0	1	20	0	0	0
18	5	3	0	3	60	0	0	0
19	6	0	0	0	0	0	0	0
20	8	1	0	0	12	0	0	0
21	7	0	0	0	0	0	0	0
22	8	1	0	1	12	0	0	0
23	3	0	0	0	0	0	0	0
24	2	0	0	0	0	0	0	0
Total	147	26	2	28	19	4	0	1

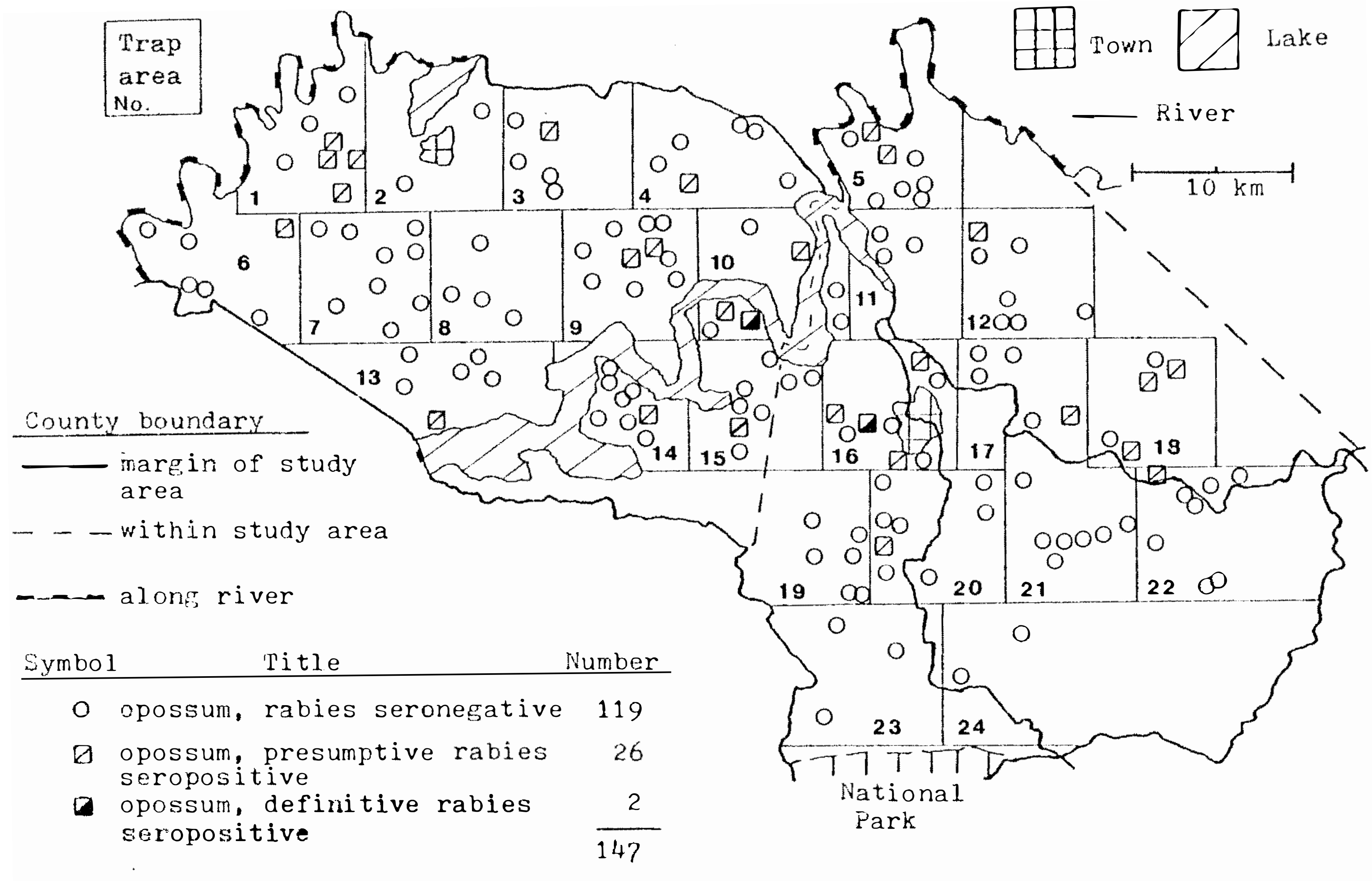


Fig. 30. Location of the 147 opossums tested for rabies antibodies in trap areas 1-24, 1975. Contiguous symbols represent animals at the same site.

(SN) titers of 1:16. These opossums were located in trap areas 10 and 16. Rabies seropositive animals appeared to be common in these two trap areas. Three of the seven opossums sampled in trap area 10 were rabies seropositive as were four of the eight opossums captured in trap area 16. These seven rabies seropositive opossums were in the same general region of the study area where four DRSP opossums were found during 1974.

As seen in 1974 most of the rabies seropositive opossums in Cocke County and southern Jefferson County appeared to have a positive association with major rivers. The PRSP opossums in trap areas 10, 13, 14, and 15 were all near the French Broad River which was expanded to form Douglas Lake. South of the junction of the French Broad and Pigeon rivers in trap area 16, PRSP opossums were captured near the former river in trap areas 17, 18, and 22 and along the latter in trap area 20. The two PRSP opossums in trap area 5 were located near the Nolichucky River.

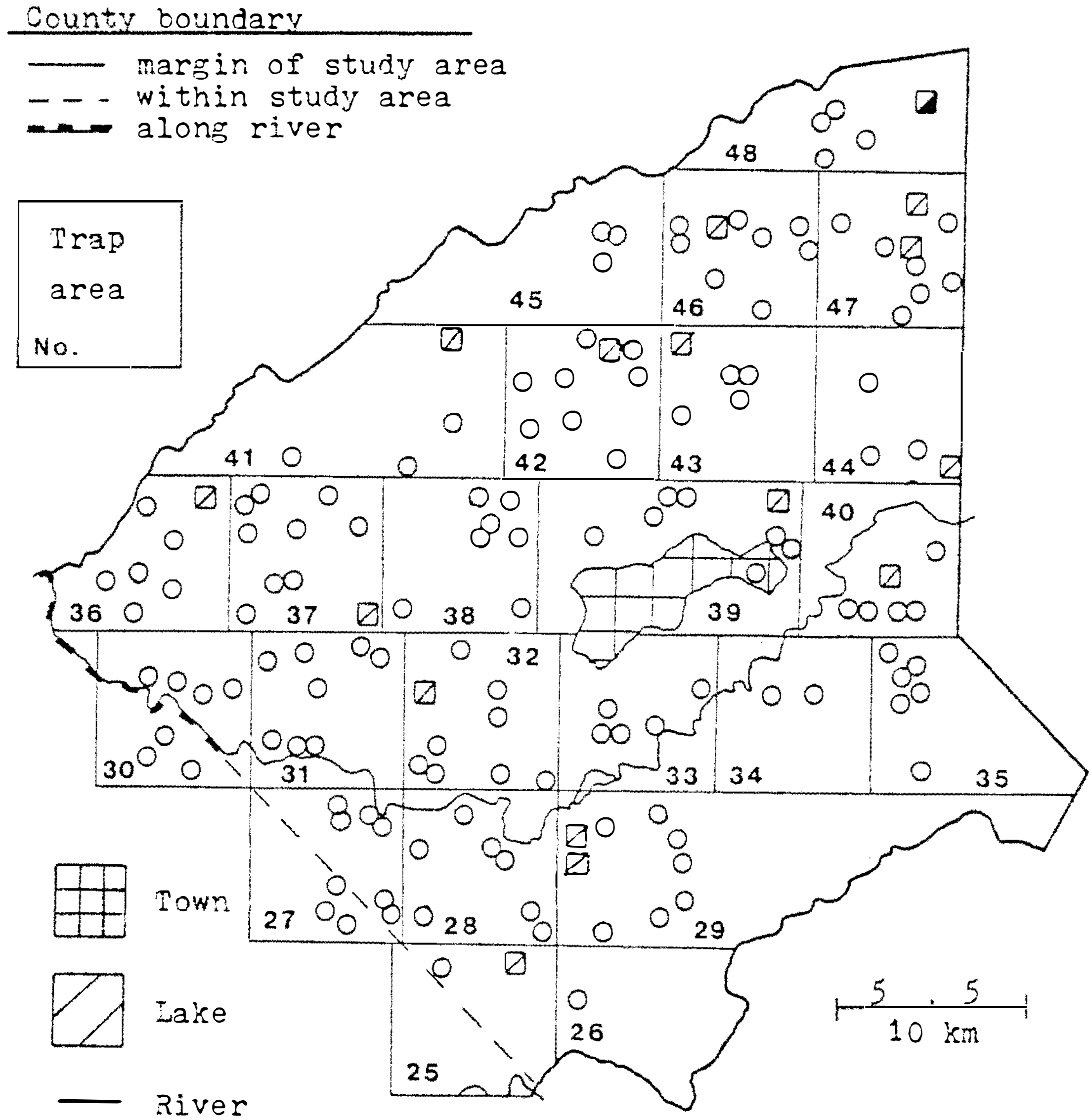
The PRSP opossums located in northern Jefferson County reflected, to a degree, the locations of past and future reported rabies cases. The four PRSP opossums in trap area 1 and the single PRSP opossum in the northeastern part of trap area 6 were located near the seven rabid striped skunks reported during the 1973-1974 period in trap areas 1 and 2. One of these PRSP opossums in trap area 1 was a juvenile female which had been born in a spring free of reported rabies cases. The PRSP opossum in trap area 4 was approximately 1.6 km from the site of the rabid striped skunk reported during June 1974. The PRSP opossum in trap area 3 was less than 2 km from the site of the rabid gray fox reported during December 1976.

During 1975 there was a single reported rabies case, a horse, in trap areas 25-48 (Table 39), and only two reported rabies cases occurred in these areas during the 1973-1975 period. However, during the 1975 survey, rabies seropositive opossums constituted 11 percent (16/151) of the sample. These seropositive animals were located in 58 percent (14/24) of the trap areas, the same percentage found in trap areas 1-24 during 1975. The capture sites of the 151 opossums tested are shown in Fig. 31.

Of the 16 rabies seropositive opossums captured in trap areas 25-48 during 1975, eight were located 6.5 km or less from the site of a reported rabies case during the following year. The single PRSP opossum collected in trap area 46 was captured at the same site as a PRSP opossum from 1973 and located less than 6 km from the site of rabies case 76-2. The two PRSP opossums found in trap area 47 were the only seropositive animals captured in this area during the study. One of these seropositive opossums in trap area 47 was captured 1.2 km from the site of rabies case 76-9, the other PRSP opossum was 2.5 km from rabies case 76-1. The DRSP opossum in trap area 48 was less than 5 km from rabies case

Table 39. Results of the 1975 serum survey among opossums in trap areas 25-48 in relation to reported rabies cases among all species during the 1974-1976 period.

Trap area	Number of opossums					Reported rabies cases		
	Tested	PRSP	DRSP	All seropositives				
				Number	Percent	1974	1975	1976
25	2	1	0	1	50	0	0	0
26	1	0	0	0	0	0	0	0
27	9	0	0	0	0	0	0	0
28	7	0	0	0	0	0	0	0
29	9	2	0	2	22	0	0	0
30	7	0	0	0	0	0	0	0
31	8	0	0	0	0	0	0	0
32	9	1	0	1	11	0	0	0
33	5	0	0	0	0	0	0	0
34	2	0	0	0	0	0	0	1
35	6	0	0	0	0	0	0	1
36	7	1	0	1	14	0	0	0
37	10	1	0	1	10	0	0	0
38	7	0	0	0	0	0	0	0
39	8	1	0	1	12	0	0	0
40	6	1	0	1	17	0	0	2
41	4	1	0	1	25	0	0	0
42	9	1	0	1	11	0	0	0
43	5	1	0	1	20	0	0	4
44	4	1	0	1	25	0	0	4
45	3	0	0	0	0	1	1	0
46	9	1	0	1	11	0	0	2
47	9	2	0	2	22	0	0	2
48	5	0	1	1	20	0	0	0
Total	151	15	1	16	11	1	1	17



Symbol	Title	Number
○	opossum, rabies seronegative	135
⊘	opossum, presumptive rabies seropositive	15
◩	opossum, definitive rabies seropositive	1
		151

Contiguous symbols represent animals at the same site

Fig. 31. Location of the 151 opossums tested for rabies antibodies in trap areas 25-48, 1975.

76-9, located in trap area 47. The PRSP opossum in trap area 43 was less than 6.5 km from the four rabid striped skunks reported in that area during 1976. The PRSP opossum in trap area 44 was approximately 2 km from rabies case 76-5. The PRSP opossum in trap area 39 was about 3.2 km from rabies case 76-10, and the PRSP opossum in trap area 40 was approximately 2.5 km from rabies case 76-4.

In trap area 45 rabies seropositive opossums had been abundant during 1973 (25 percent of sample) and 1974 (50 percent of sample). However, in 1975 the three opossums tested, two adults and one juvenile, were rabies seronegative.

Trap area 48 which was just north of the areas with several reported rabies cases during 1972 and 1976 contained rabies seropositive opossums for the second consecutive year. During 1974, 43 percent of the opossums captured in trap area 48 were rabies seropositive, and in 1975, 20 percent were seropositive, including the only DRSP opossum in trap areas 25-48. This DRSP opossum had an SN titer of 1:50.

The eight seropositive opossums collected during 1975 which were not geographically associated with reported rabies cases in 1976 were captured in trap areas 25, 29, 32, 36, 37, 41, and 42. However, three of these opossums were associated geographically with seropositive opossum from previous years. The PRSP opossum in trap area 29 was captured at the same site as a PRSP opossum from 1974. The PRSP opossum captured in trap area 36 was approximately 1.5 km from the DRSP opossum found in trap area 37 during 1974. The PRSP opossum captured in trap area 33 was located less than 2.5 km from both the PRSP opossums found in that area during 1974.

It is interesting to note that two of the 16 seropositive opossums collected in trap areas 25-48 during 1975 were captured at the same sites where seropositive opossums had been captured in previous years. One of these sites was in trap area 46 which had one of the highest number of reported rabies cases over the 1972-1976 period, and the other site was in trap area 29 where no reported rabies cases occurred during the five-year period.

The presence of rabies seropositive opossums among the trap areas during 1975 did portend, to some extent, the occurrence of rabid animals during 1976. Among the seven trap areas which contained reported rabies cases during 1976, five contained rabies seropositive opossums during 1975. Only trap areas 34 and 35 experienced reported rabies cases during 1976 and lacked seropositive opossums during 1975. However, seropositive opossums did occur in nine trap areas which did not contain reported rabies cases during 1976.

The analyses of the 57 serum samples from free-roaming domestic cats revealed that seven (12.3 percent) were PRSP and 50 (87.7 percent) were seronegative (Table 40). The percentage of cats found to be PRSP was slightly less than the percentages of opossums found to be rabies seropositive during 1973 (15.4 percent), 1974 (22.4 percent), and 1975 (14.8

Table 40. Results of the serum survey among free-roaming domestic cats in the study area, 1975.[a]

Trap area	Weight (kg) More than or equal to: / Less than: / Sex	1.4 / 2.3		2.3 / 3.2		3.2 / 4.1		4.1 / 5.0		Total		
		M	F	M	F	M	F	M	F	M	F	
2	RSN	-	-	-	-	-	1	-	-	-	1	1
3	RSN	-	-	-	2	-	-	-	-	-	2	2
4	RSN	-	-	-	-	-	1	-	0	-	1	1
	PRSP						0		1*		1*	1*
5	RSN	-	-	-	-	1	-	-	-	1	-	1
8	RSN	-	1	-	1	-	-	-	-	-	2	2
	PRSP		0		1*						1*	1*
10	RSN	-	-	-	-	0	1	-	-	0	1	1
	PRSP					1*	0			1*	0	1*
12	RSN	-	1	1	-	-	-	-	-	1	1	2
13	RSN	-	-	-	-	1	-	1	-	2	-	2
15	RSN	-	-	-	1	-	-	-	-	-	1	1
16	RSN	-	-	-	1	-	-	-	-	-	1	1
	PRSP				1*						1*	1*
17	RSN	-	-	0	-	-	-	-	-	0	-	0
	PRSP			1*						1*		1*
18	RSN	-	-	-	2	-	-	-	-	-	2	2
19	RSN	-	-	-	-	1	-	-	-	1	-	1
20	RSN	-	-	-	2	-	-	-	-	-	2	2
23	RSN	-	-	1	-	1	-	-	-	2	-	2
24	RSN	-	-	1	-	-	-	-	-	1	-	1
25	RSN	-	-	-	-	3	-	-	-	3	-	3
27	RSN	-	-	0	-	1	-	-	-	1	-	1
	PRSP			1*		0				1*		1*
29	RSN	-	-	1	-	1	-	-	-	2	-	2

Table 40. continued.

Trap area	Weight (kg) More than or equal to: / Less than: / Sex	1.4–2.3 M	1.4–2.3 F	2.3–3.2 M	2.3–3.2 F	3.2–4.1 M	3.2–4.1 F	4.1–5.0 M	4.1–5.0 F	Total M	Total F	Total
31 RSN		-	-	1	-	-	-	-	-	1	-	1
32 RSN		-	-	-	1	-	-	-	-	-	1	1
33 RSN		-	-	-	-	1	-	-	-	1	-	1
34 RSN		-	-	1	-	-	1	-	-	1	1	2
35 RSN		-	-	-	2	-	-	-	-	-	2	2
37 RSN		-	-	-	1	-	-	-	-	-	1	1
40 RSN		-	-	-	1	1	2	-	-	1	3	4
41 RSN		-	-	-	-	2	-	-	-	2	-	2
43 RSN		-	1	-	-	-	-	1	-	1	1	2
44 RSN		-	-	-	3	-	-	-	-	-	3	3
45 RSN		-	1	-	-	-	0	-	-	-	1	1
PRSP			0				1*				1*	1*
47 RSN		-	-	1	-	-	-	-	-	1	-	1
48 RSN		-	-	-	-	1	-	-	-	1	-	1
Subtotal	RSN	-	4	7	17	14	6	2	0	23	27	50
	PRSP	-	0	2*	2*	1*	1*	0	1*	3*	4*	7*
Weight class totals												
	RSN	4		24		20		2				50
	PRSP	0		4*		2*		1*				7*
Total tested		4		28		22		3				57

[a]The sample(s) is (are) either rabies seronegative (RSN), or presumptive rabies seropositive (PRSP *).

- = No samples tested.

percent). The percentage of PRSP males (11.5 percent) was similar to that (12.9 percent) found among females. Cats were not assigned to age classes, but were divided into four weight categories. The small numbers of cats sampled and found rabies seropositive in each weight class were not suited to statistical analysis, but the seropositive cats did not appear to be unusually abundant in any one of the four weight classes.

The locations of the 57 cats tested during 1975 are shown in Fig. 32. At least one cat was tested from 32 trap areas and the seven PRSP cats were located in seven different trap areas. Within the three counties of approximately 3,400 km^2 which composed the study area, rabies vaccinations were given to 605 cats during 1975 (Tennessee Department of Public Health 1976:17). This total included 205 cats in Jefferson County, 100 cats in Cocke County, and 300 cats in Greene County. None of the cats sampled during 1975 had any type of collar or identification tag. It was considered doubtful that any of the PRSP cats had been vaccinated. If the seven PRSP cats had all been vaccinated, they would have represented slightly more than 1 percent of all the cats vaccinated in the three-county area during 1975.

Six of the seven rabies seropositive cats had a strong positive geographical association with reported rabies cases and/or rabies seropositive opossums from 1975 and previous years. These six PRSP cats were all within 5 km of either a

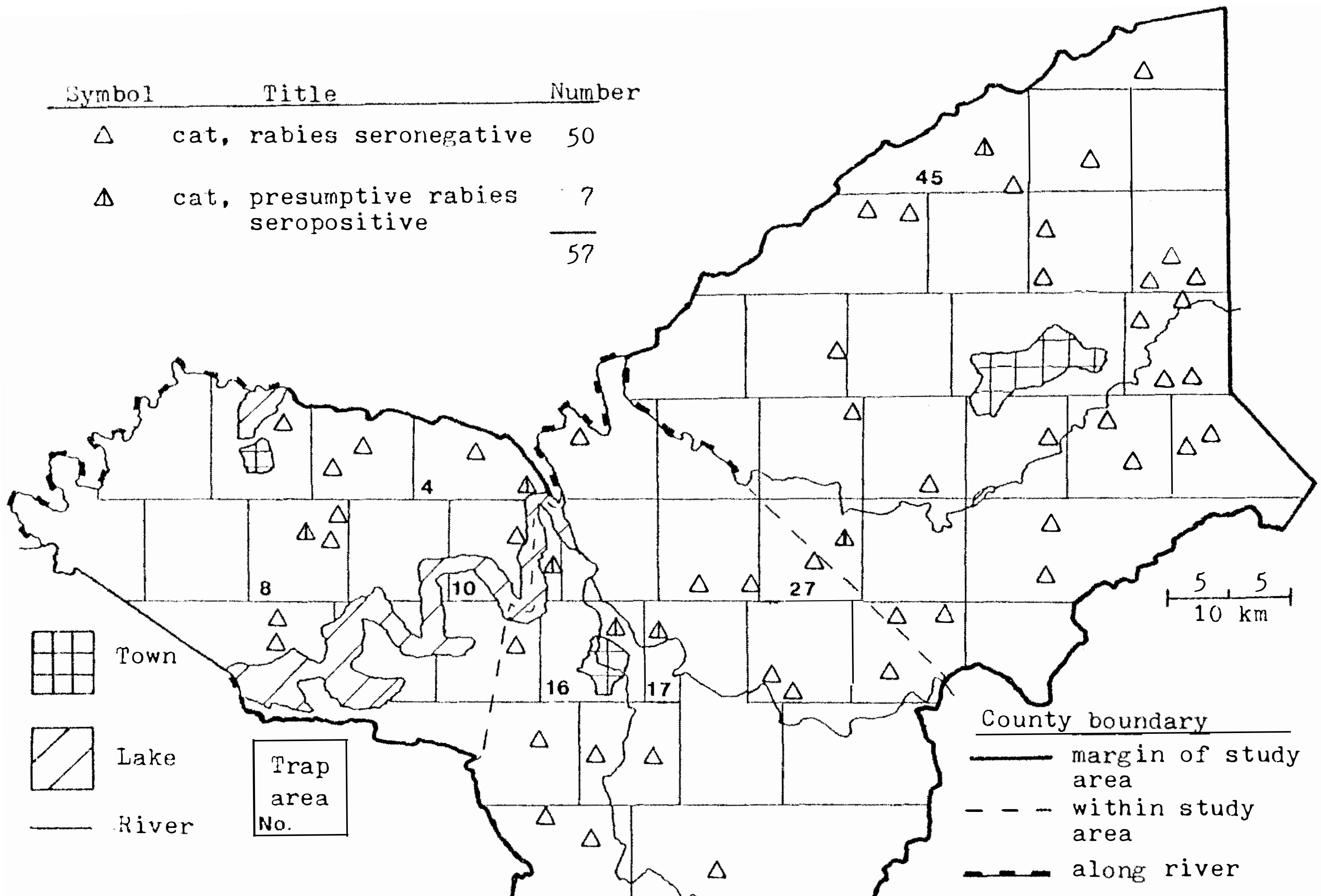


Fig. 32. Location of the 57 cats tested for rabies antibodies in the study area, 1975.

reported rabies case or a rabies seropositive opossum. Four of the PRSP cats were located along the French Broad River in trap areas 4, 10, 16, and 17. This distribution was quite similar to that found among rabies seropositive opossums during 1974 and 1975. The occurrence of four PRSP cats in this area of eastern Jefferson County and northwestern Cocke County reinforced the idea that the rabies virus might have been widely circulated in this area despite the absence of reported rabies cases.

The single PRSP cat captured in trap area 8 was interesting in that it was located approximately 2 km from both the rabid cow reported during 1972 and the PRSP opossum captured during 1973. This cat was also located only several hundred meters from the site of the rabid striped skunk reported in June of 1974. While none of the seven opossums captured in trap area 8 during the 1974-1975 period were rabies seropositive, this area did appear to have a localized, persistent focus of rabies seropositive and rabid animals which together represented one animal from four different species.

The single PRSP cat in trap area 45 was closely related geographically with two reported rabies cases and several rabies seropositive opossums. This cat, a 2.8 kg female, was captured less than 4 km from rabies case 74-3, a striped skunk, and less than 1 km from rabies case 75-1, a horse.

Only the PRSP cat captured in trap area 27 appeared to be isolated from both reported rabies cases and other rabies seropositive opossums. It should be noted that several trap areas with reported rabies cases and rabies seropositive opossums did not contain any rabies seropositive cats among those sampled. A total of 26 reported rabies cases occurred in trap areas 34, 35, 40, 43, 44, and 46, but none of the 14 cats captured in these six areas were rabies seropositive.

Serum Survey, 1976

During 1976 trapping was conducted during July and August. This trap effort consisted of 548 trap nights at 195 sites. Eight farms were used in eastern Greene County on which a rabid animal (seven striped skunks and one dog) had been found earlier in the year. The roadside trapping was restricted to established sites at which a rabies seropositive animal had been captured in previous years or near such a site. Free-roaming domestic cats were not sampled during 1976.

One juvenile striped skunk was captured on Farm M in trap area 44. This skunk was rabies seronegative. While 114 opossums were captured, serum samples were analyzed for only 53 opossums. The serum analyses revealed that four (7.5 percent) of the opossums were PRSP and 49 (92.4 percent) were rabies seronegative (Table 41). The four PRSP opossums had RFFIT titers of 1:5, 1:9, 1:16, and 1:29. Seventy-two

Table 41. Results of the 1976 serum survey among opossums by sex and weight class.

Age	Juvenile				Subadult		Adult										
	Weight classes are defined in Table 24, page 107																
Wt.	1		2		3		4		5		6		7		Total		
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
Sample	0	0	4	1	5	6	2	8	1	12	2	8	1	3	15	38	53
% Total	-	-	8	2	9	11	4	15	2	22	4	15	2	6	28	72	
Presumptive rabies seropositive (PRSP)																	
Number	-	-	0	0	0	1	0	1	0	0	0	2	0	0	0	4	4
% Sample	-	-	-	-	-	17	-	12	-	-	-	25	-	-	-	10	8
% Weight class	-		-		9		10		-		20		-				

percent (38/53) of the opossums sampled were female, but all the PRSP animals were females. Data were not sufficient for an analysis by age class, but three of the four PRSP opossums were adults, and the fourth was a subadult. Detailed data on the serum survey among opossums by sex, weight class, and trap area or farm are given in Appendix P.

The locations of the 53 opossums and the single striped skunk tested during 1976 are shown in Fig. 33. Only seven opossums were tested from trap areas 1-24, and all of these were rabies seronegative. These seven opossums were all collected at sites where a DRSP opossum had been captured in previous years. However, these data seemed insufficient to determine whether the concentrations of rabies seropositive animals found in trap areas 1, 10, 11, and 16 during previous years had ceased to exist.

In trap areas 25-48 the four PRSP opossums were located on Farm GR (trap area 46), Farm F (trap area 35), trap area 40, and trap area 35. Due to the trapping procedure it was expected that any seropositive animals would be located near reported rabies cases. The PRSP opossum captured at a roadside site in trap area 35 was 1.6 km from rabies case 76-8, and the PRSP opossums in trap area 40 was 1.5 km from the site of rabies case 76-5.

Among the eight farms trapped during 1976, the average time between the reported rabies case and the initiation of trapping was 83 days with a range between 18 days (Farm GO)

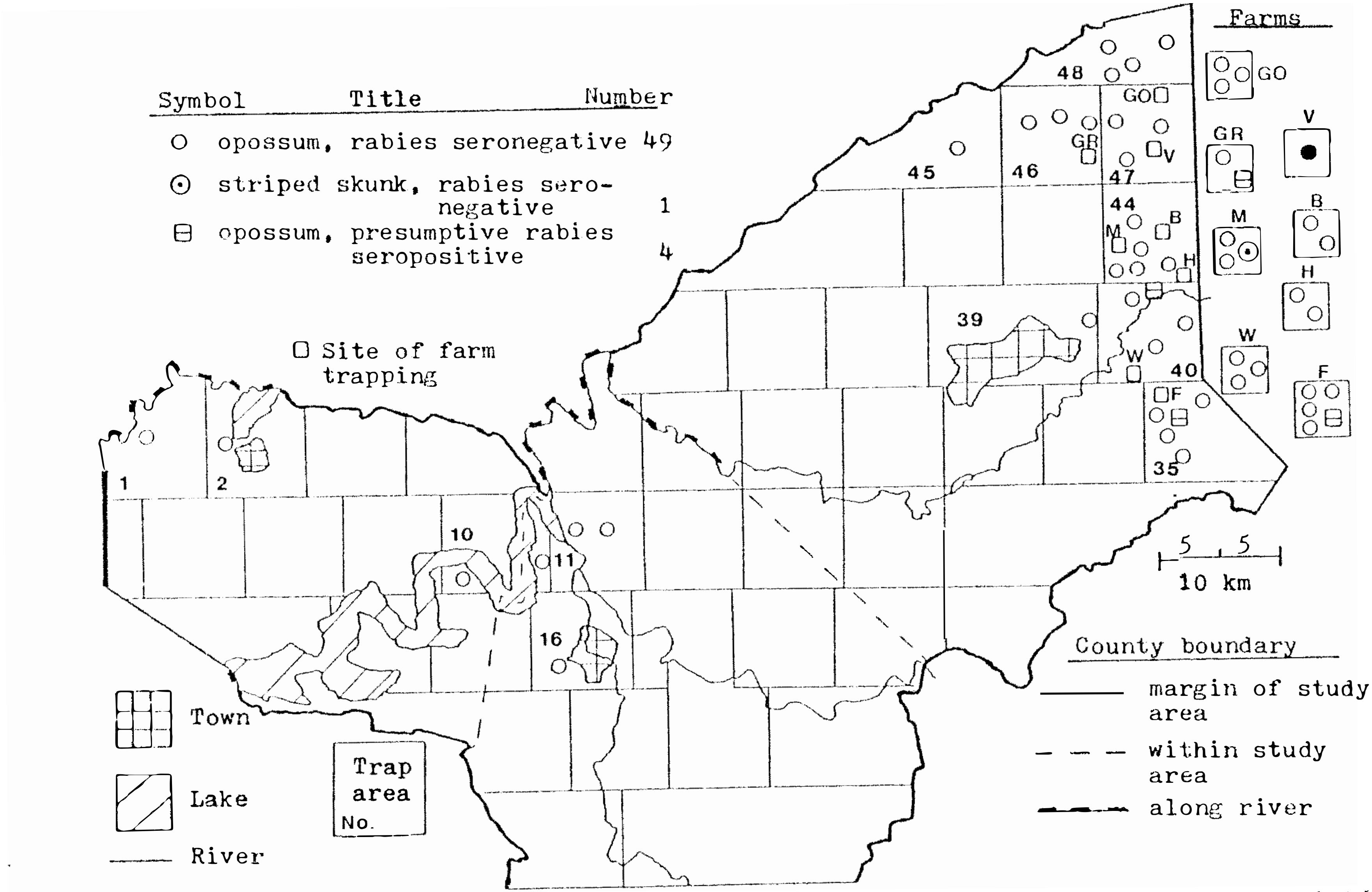


Fig. 33. Location of the 54 animals tested for rabies antibodies in the study area, 1976.

and 136 days (Farms GR and V). Considering the data from these farms as a unit, only 9.5 percent (2/21) of the animals captured were rabies seropositive. This percentage was much lower than that found on the two farms trapped in trap area 1 during 1974. These two farms, Farms C and K, were trapped an average of 46 days (61 and 31 days) after the rabid skunk was reported, and 62 percent (8/13) of the opossums tested were rabies seropositive. It is possible that the greater time span between the occurrence of the rabid animal on the Greene County farms contributed to the lower percentage of rabies seropositive animals found on these farms. There was another difference between the farm trapping in 1974 and 1976 in that five rabid skunks were reported from trap area 1 during 1973, and during 1974 that area was experiencing its second consecutive spring of rabies cases among striped skunks. However, Greene County which had a skunk rabies outbreak during 1972 was relatively free of reported rabies cases during 1973-1975 period with no reported rabies cases in any of the trap areas where farm trapping was conducted during 1976. The influence of the time delay between the occurrence of the rabid animal and trapping and the number of rabid animals in the year prior to trapping on the percentage of animals with rabies antibodies found on these farms could not be determined.

Serological Results Among Opossum Pouched Young

In an effort to determine the immunological relationship between the female opossum and her pouched young, a small blood sample was collected from one nursing young in each of nine litters at the time the female was sampled. Among these 18 samples, none were found to be DRSP, but three were PRSP (Table 42). Considering the two immunological categories, RSN and PRSP, present among the mother-young samples, three of the four possible permutations were found. None of the pairs contained two PRSP samples. There were two cases with PRSP young which had rabies seronegative mothers, and one case of a PRSP mother with a rabies seropositive young.

In evaluating the distribution of rabies seropositive opossums, the immunological character of the pouched young was not considered. The two rabies seronegative females with PRSP young were designated as seronegative captures.

The two cases with PRSP young from a RSN mother could not be explained conclusively. Bell et al. (1970:1055) cited one of their earlier studies which demonstrated that rabies antibodies could be transferred from female mice to their offspring by suckling. They also noted that this passive immunity acquired by suckling reached a peak at the time of weaning and then decreased slowly. The results of the present study may have been influenced by the presence of nonspecific immunological substances, or the special marsupial physiology of opossum pouched young.

Table 42. Results of serum analysis among nine adult female opossums and one of their pouch young.

Date	Location (trap area, quadrant)	Rabies serology	
		Ad. female (mother)	Pouch young
April 1974	9 SE	seronegative	seronegative
April 1974	9 SE	seronegative	seronegative
April 1974	14 NW	seronegative	seronegative
April 1974	38 NE	seronegative	seronegative
April 1974	38 NE	seronegative	presumptive rabies seropositive
May 1974	35 NW	seronegative	seronegative
May 1975	5 NW	presumptive rabies seropositive	seronegative
June 1975	33 NW	seronegative	presumptive rabies seropositive
July 1975	15 NE	seronegative	seronegative

Analysis of Opossum Salivary Gland Samples

A sample of salivary gland tissue was collected along with the blood sample from all opossums and the single striped skunk collected during the 1975-1976 period. After the serum analyses were completed, the salivary gland samples from the four PRSP opossums from 1976 and the three DRSP opossums from 1975 were selected for FRA analysis. Three rabies seronegative opossums were chosen from the females collected during 1976 to serve as controls. Females were used as controls because the seven seropositive animals were all females.

These 10 tissue samples which had been stored at -70° C were tested during December 1976. Only one sample was conclusively found to contain rabies antigen (Table 43). This sample was from a juvenile female which had the highest RFFIT titer among the four PRSP opossums of 1976. The other nine samples were considered to be negative for rabies antigen.

While the three DRSP opossums from 1975 were classified as negative, two of these samples showed faint traces of fluorescence similar in appearance to antigenic "dust." Kissling (1975:409) stated that

> rabies antigen in salivary gland tissue usually occurs in smaller, more irregular masses than those observed in brain tissue; dustlike antigen is very commonly found.

Therefore, these two tissue samples may have contained rabies antigen at the time of collection, but the extensive period

Table 43. Results of tests for the presence of rabies antigen in the salivary gland samples from 10 opossums collected in the study area.[a]

Month of capture	Location (trap area, quadrant)	Sex	Weight (kg)	Reproductive status	Rabies serology	Test for rabies antigen: Fluorescent rabies antibody (FRA)	Test for rabies antigen: Mouse inoculation
May 75	48 NE	F	2.2	with young	DRSP	negative[b]	-
May 75	10 SW	F	2.3	no young	DRSP	negative[b]	-
July 75	16 SW	F	2.4	no young	DRSP	negative	-
July 76	46 SE Farm GR	F	2.5	with young	PRSP RFFIT 1:16	negative	-
July 76	35 NW Farm F	F	2.6	with young	PRSP RFFIT 1:9	negative	-
Aug 76	35 NW	F	1.6	no young	PRSP RFFIT 1:5	negative	-
Aug 76	40 NE	F	1.0	no young	PRSP RFFIT 1:29	positive	negative
Controls							
July 76	35 NW Farm F	F	1.7	with young	negative	negative	-
Aug 76	47 NW	F	2.3	with young	negative	negative	-
Aug 76	48 SW	F	2.3	no young	negative	negative	-

[a]FRA test done 7-8 December 1976.

[b]Faint traces of fluorescence observed.

of storage could have reduced the amount of detectable antigen in these samples. The length of storage or other factors could have reduced the ability to produce positive results by the mouse inoculation test.

These data suggest that a portion of the rabies seropositive opossums in the study areas had rabies antigen in their salivary glands. Whether such animals were clinically rabid or progressing toward clinical rabies is unknown. These data also do not allow for establishing or rejecting the existence of chronic rabies carriers within the opossum population, but the possibility of opossums as important rabies vectors cannot be excluded. However, there is a strong suggestion that rabies infected opossums may not be "dead-ends" in the natural circulation of the rabies virus, but these animals may serve to transmit rabies by either bite or nonbite routes.

Total Serum Survey Data, Sex and Age Considerations

Among the three species included in the serum survey, the striped skunk constituted the smallest sample size. The fact that only three striped skunks were tested prevented any conclusive evaluation of the prevalence of seropositive animals within the striped skunk population. However, one of the three striped skunks sampled was DRSP, and it would seem possible to postulate that rabies seropositive striped skunks existed in the study area and may have constituted a sizeable portion of the skunk population. Since free-roaming domestic cats were only sampled during 1975, the data from that year represented a summary of the rabies serology for this species.

During the four years of the serum survey, 608 opossums were tested for the presence of rabies antibodies (Table 44). The percentages of PRSP and DRSP among males and females were quite similar. The total number of seropositive animals constituted 15.7 percent (35/223) of the males and 17.1 percent (66/385) of the females. These data suggest that there was no sexual differentiation in the degree of exposure to the rabies virus.

The percentage of rabies seropositive animals among the seven weight classes varied widely. Seropositive animals constituted only 3 percent (1/35) of the opossums in weight class 1, but in weight class 5, 22 percent (37/171) of the opossums were rabies seropositive. Adults had a significantly higher number of rabies seropositive animals than nonadults ($P < .05$).

Some intriguing trends can be observed in the data regarding PRSP opossums (Fig. 34). PRSP opossums were not found among the 18 females of weight class 1, but starting in weight 2 the percentages of PRSP females increased steadily up to weight class 5. In contrast to this pattern, PRSP males in weight class 1 constituted 6 percent (1/17) of the sample, and from this class to weight class 4 the percentages of PRSP males dropped steadily. Following this decline there

Table 44. Summary of serum survey data among opossums by sex and weight class, 1973-1976.

Age	Juvenile				Subadult		Adult										
	Weight classes are defined in Table 24, page 107																
Wt.	1		2		3		4		5		6		7		Total		
Sex	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
Sample	17	18	25	12	30	38	32	102	37	134	51	64	31	17	223	385	608
% Total	3	3	4	2	5	6	5	17	6	22	8	10	5	3	37	63	
Presumptive rabies seropositive (PRSP)																	
Number	1	0	1	1	1	4	1	16	11	22	10	8	6	3	31	54	85
% Sample	6	-	4	8	3	10	3	16	30	16	20	12	20	18	14	14	14
% Weight class	3		5		7		13		19		16		19				
Definitive rabies seropositive (DRSP)																	
Number	0	0	0	0	0	0	0	6	1	3	2	3	1	0	4	12	16
% Sample	-	-	-	-	-	-	-	6	3	2	4	5	3	-	2	3	3
% Weight class	-		-		-		4		2		4		2				
All rabies seropositives, by weight class																	
Number	1		2		5		23		37		23		10		35	66	101
% Weight class	3		5		7		17		22		20		21		16	17	17

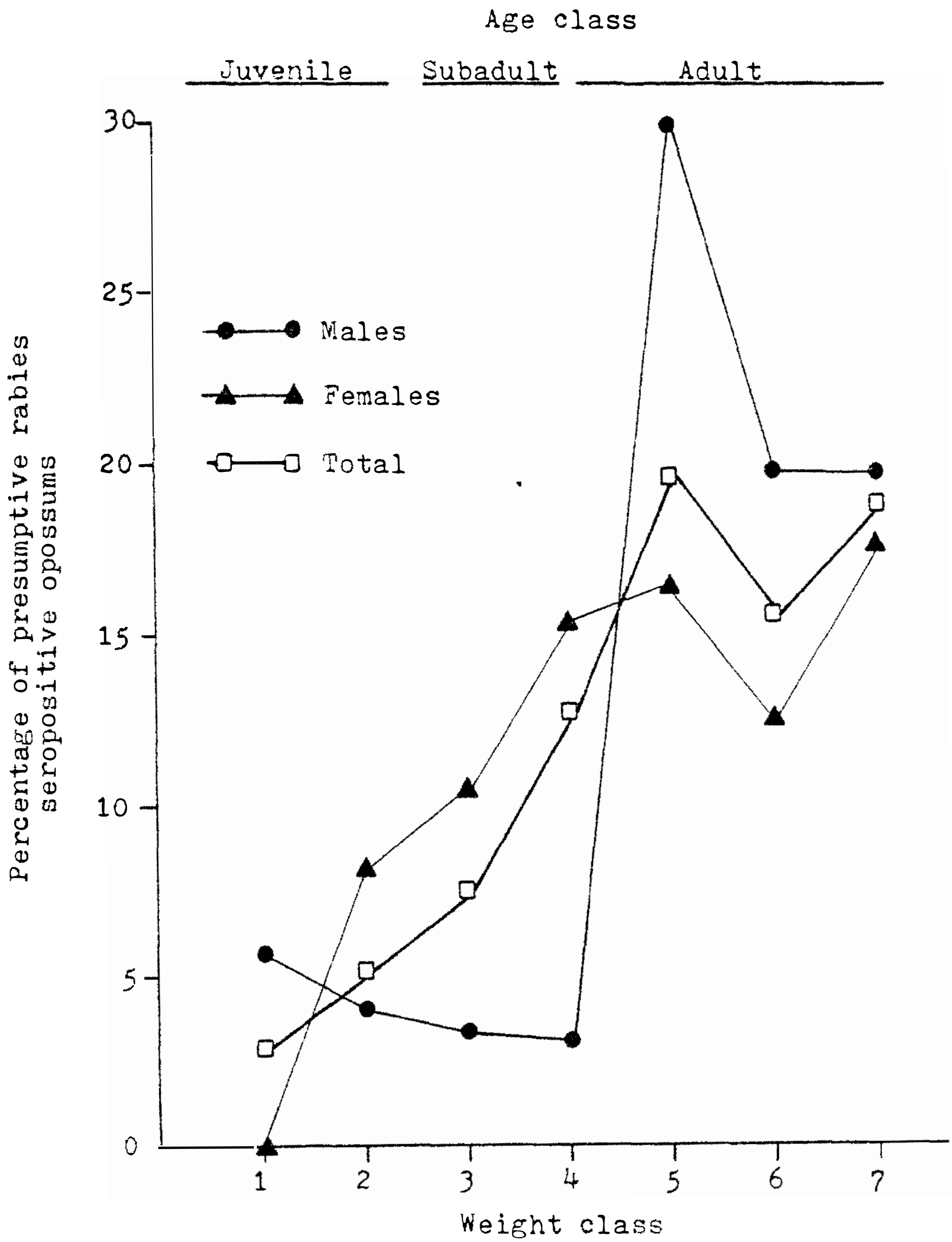


Fig. 34. Percentage of presumptive rabies seropositive opossums among the total number of opossums tested in the seven weight classes, 1973-1976. Weight classes are defined in Table 24, page 107.

was a tenfold increase in the percentage of PRSP males between weight class 4 (3 percent) and weight class 5 (30 percent). It may be significant to note that the time between these two weight classes represents a period when the males age from approximately 10 months to over 11 months. This span of time corresponds, to some extent, with the winter breeding season in which all young of the preceding year may participate. It is conceivable that many young males are exposed to rabies during the mating season. The source of this exposure could be females or rival males encountered during mating activities. As the opossums gain more weight and become part of weight classes 6 and 7, the percentages of PRSP individuals among males and females become increasingly similar.

The data regarding DRSP opossums are different from those for PRSP opossums (Fig. 35). There were no DRSP individuals found among juveniles or subadults of either sex, and all DRSP males weighed more than 1.82 kg (4 lb). In most cases these DRSP opossums would have been in their second year of life. As females moved from the subadult to adult age class, there was a sharp rise in the percentage of DRSP individuals, but no change occurred among males. In weight classes 5-6 the percentages of DRSP males and females were similar. The absence of DRSP females in weight class 7 may have reflected the scarcity of such large females.

Considering the combined data for males and females,

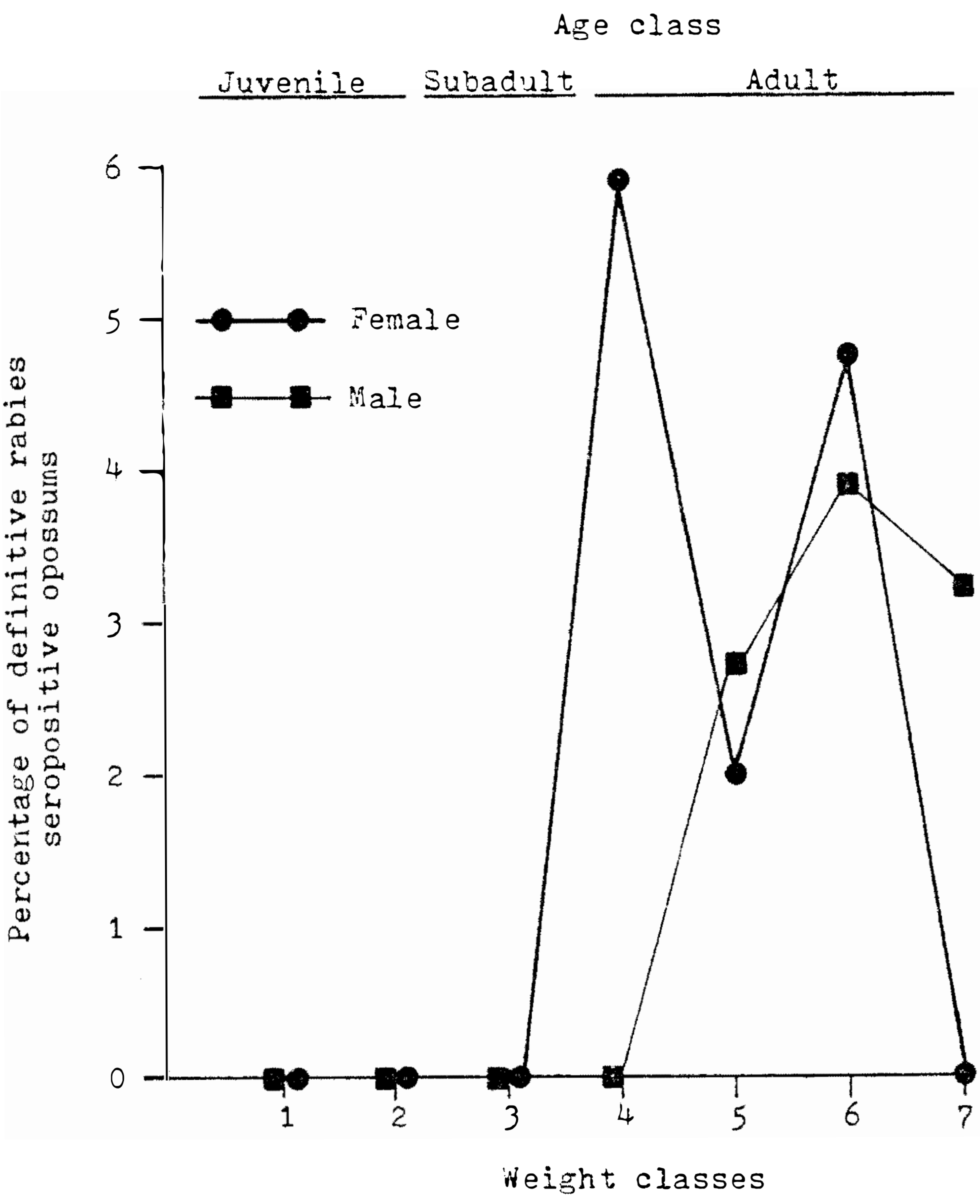


Fig. 35. Percentage of definitive rabies seropositive opossums among the total number of opossums tested in the seven weight classes, 1973-1976. Weight classes are defined in Table 24, page 107.

there was a distinct increase in the proportion of PRSP individuals from the lowest weight class to weight class 5, the time of early adulthood (Fig. 36). DRSP opossums were found only among adults, and the percentages of DRSP individuals in the four weight classes considered to be adults were fairly uniform. When the percentages of all seropositive opossums among the weight classes are considered, the greatest increase came between weight class 3 (7 percent) and weight class 4 (17 percent). This period coincides with the time designated to represent the transition from the subadult to adult stage of life for the opossum.

Total Serum Survey Data, Geographical Considerations

During the four-year serum survey, at least one rabies seropositive animal was collected by roadside trapping in 83 percent (40/48) of the trap areas (Table 45). Among these 40 trap areas the percentages of rabies seropositive animals ranged from 5 percent in trap areas 27 and 44 to 46 percent in trap area 16. Both trap areas 27 and 16 were free of reported rabies cases during the 1972-1976 period.

The percentage of seropositive animals was significantly higher ($P < .05$) among opossums captured on farms near the site of a reported rabies case than among the opossums collected in systematic roadside trapping. Among the 33 opossums collected at farm sites 10 (30 percent) were rabies seropositive. Among the 575 opossums sampled from roadside sites 91 (16 percent) were rabies seropositive. However, rabies

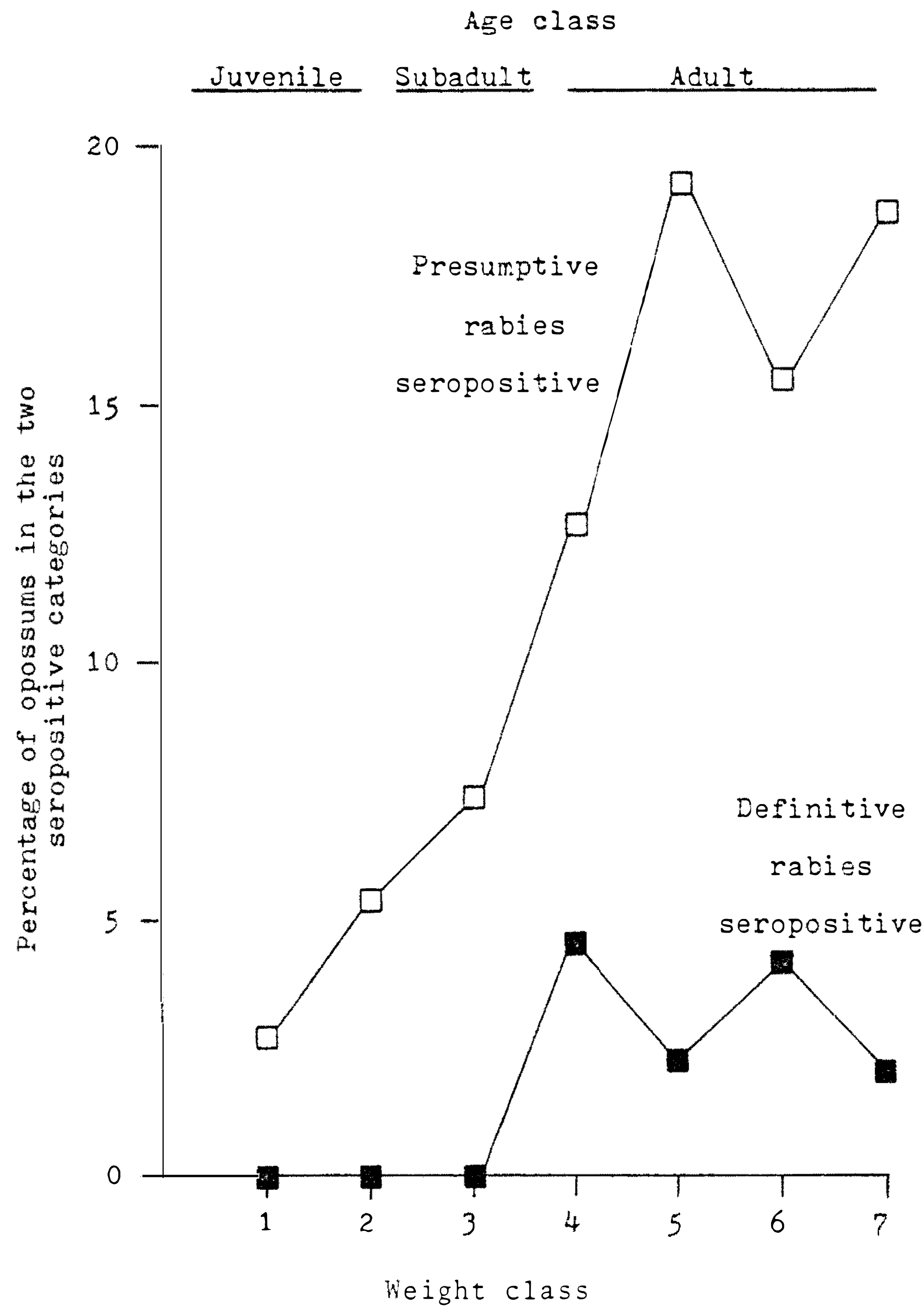


Fig. 36. Percentage of presumptive rabies seropositive and definitive rabies seropositive opossums (both sexes) among the total number of opossums tested in the seven weight classes, 1973-1976. Weight classes are defined in Table 24, page 107.

Table 45. Data summary of serum analysis among opossums (Opos), free-roaming domestic cats, and striped skunks (Sk) captured at roadside sites in the 48 trap areas, 1973-1976.[a]

Trap	1973	1974		1975		1976		% rabies sero-
area	Opos	Sk	Opos	Opos	Cat	Opos	Total	positive
1	2/4	-	0/12	4/ 7	-	0/1	6/24	25
2	-	-	2/ 3	0/ 2	0/1	0/1	2/ 7	29
3	0/3	-	1/ 3	1/ 5	0/2	-	2/13	15
4	-	-	2/ 6	1/ 6	1/2	-	4/14	29
5	0/5	-	2/ 5	2/ 8	0/1	-	4/19	21
6	-	-	1/ 4	1/ 6	-	-	2/10	20
7	-	-	0/ 4	0/ 8	-	-	0/12	0
8	1/2	-	0/ 3	0/ 4	1/3	-	2/12	17
9	-	-	0/ 5	2/10	-	-	2/15	13
10	-	-	2/ 7	3/ 7	1/2	0/2	6/18	33
11	0/3	-	3/ 8	0/ 3	-	0/2	3/16	19
12	-	-	0/ 3	1/ 7	0/2	-	1/12	8
13	1/1	-	0/ 2	1/ 6	0/2	-	2/11	18
14	-	-	0/ 2	1/ 8	-	-	1/10	10
15	0/3	-	1/ 2	1/ 8	0/1	-	2/14	14
16	-	-	1/ 2	4/ 8	1/2	0/1	6/13	46
17	-	-	0/ 3	1/ 5	1/1	-	2/ 9	22
18	0/2	-	0/ 3	3/ 5	0/2	-	3/12	25
19	-	-	0/ 6	0/ 6	0/1	-	0/13	0
20	-	-	1/ 3	1/ 8	0/2	-	2/13	15
21	0/2	-	0/ 7	-	-	-	0/ 9	0
22	1/2	-	0/ 2	1/ 8	-	-	2/12	17
23	0/3	-	1/ 3	0/ 3	0/2	-	1/11	9
24	0/2	-	0/ 1	0/ 2	0/1	-	0/ 6	0
Subtotal trap areas 1-24								
	5/32	-	17/92	28/147	5/27	0/7	55/305	18
25	0/4	-	0/ 1	1/ 2	0/3	-	1/10	10
26	-	-	2/ 4	0/ 1	-	-	2/ 5	40
27	0/3	-	0/ 4	0/ 9	1/2	-	1/18	5
28	1/2	-	0/ 5	0/ 7	-	-	1/14	7
29	-	-	1/ 6	2/ 9	0/2	-	3/17	18
30	-	-	0/ 2	0/ 7	-	-	0/ 9	0

Table 45. continued.

Trap area	1973 Opos	1974 Sk	1974 Opos	1975 Opos	1975 Cat	1976 Opos	Total	% Rabies sero-positive
31	-	-	0/ 7	0/ 8	0/1	-	0/16	0
32	-	-	2/ 6	1/ 9	0/1	-	3/16	19
33	-	-	1/ 4	0/ 5	0/1	-	1/10	10
34	0/2	-	0/ 2	0/ 2	0/2	-	0/ 8	0
35	0/1	-	1/ 3	0/ 6	0/2	1/5	2/17	12
36	0/5	-	0/ 1	1/ 7	-	-	1/13	8
37	0/1	-	1/ 2	1/10	0/1	-	2/14	14
38	0/2	-	0/ 3	0/ 7	-	-	0/12	0
39	0/2	-	0/ 2	1/ 8	-	0/1	1/13	8
40	-	-	2/ 6	1/ 6	0/4	1/4	4/20	20
41	-	0/1	1/ 2	1/ 4	0/2	-	2/ 9	22
42	-	-	1/ 3	1/ 9	-	-	2/12	17
43	-	-	0/ 2	1/ 5	0/2	-	1/ 9	11
44	-	-	0/ 7	1/ 4	0/3	0/5	1/19	5
45	1/4	-	3/ 6	0/ 3	1/2	0/1	5/16	31
46	3/4	1/1	0/ 2	1/ 9	0/1	0/3	5/20	25
47	0/1	-	-	2/ 9	-	0/3	2/13	15
48	0/2	-	3/ 7	1/ 5	0/1	0/4	4/19	21
Subtotal trap areas 25-48								
	5/33	1/2	18/87	16/151	2/30	2/26	44/329	13
Total for study area, trap areas 1-48								
	10/65	1/2	35/179	44/298	7/57	2/33	99/634	16
Species totals								
Opossum	10/65		35/179	44/298		2/33	91/575	16
Cat					7/57		7/ 57	12
Striped skunk		1/2					1/ 2	50

[a]Data show number of rabies seropositive animals/ number of animals tested.

seropositive opossums were found in 83 percent of the 48 trap areas, but only four of the 10 farms sampled contained rabies seropositive opossums.

In trap areas 1-24 which consisted primarily of Jefferson and Cocke counties, 18 percent (55/305) of the animals (opossums and cats) collected by roadside trapping were rabies seropositive. This percentage was larger than the 13 percent (44/329) seropositive animals (opossums, cats, and striped skunks) collected along roadsides in trap areas 25-48 which consisted primarily of Greene County. However, these percentages were not significantly different ($P > .10$). These data did not reflect the distribution of reported rabies cases during the 1972-1976 period. During these five years 79 percent (41/52) of all reported rabies cases in the study area occurred in Greene County. Based on these data there was a highly significant concentration of reported rabies cases in Greene County ($P < .001$).

There was no statistical association between those trap areas with a high capture rate and the trap areas with a high percentage of seropositive animals. Because rabies transmission is considered to occur by direct contact between the diseased host and other susceptible hosts, high population densities might be expected to facilitate transmission and produce a higher percentage of seropositive animals in the trap areas with abundant animal populations. While the calculated capture rate, captures per 100 trap nights, is not a definitive measure of population density, this figure does reflect, to some extent, the relative abundance of animals among the 48 trap areas.

To evaluate the relationship between capture rates and rabies seropositive percentages the data from 1975 among opossums was considered because (1) the largest sample was collected in that year, (2) each trap area was used only once, and (3) only one reported rabies case occurred in the study area. The 48 trap areas were ranked from the highest capture rate, 34.3 in trap area 9, to the lowest, 3.1 in trap area 26 (Appendix K, Table 66). In order to reduce the number of ties (areas with exactly equal capture rates) the areas in rank order were grouped into 11 sets with four or five trap areas in each set. The serum survey data among opossums for the trap areas in each set were combined, and a single percentage of seropositive opossums was calculated for each of the 11 sets of trap areas. These 11 percentages were also ranked from the highest to the lowest. Among the 11 sets of trap areas the ranks for capture rate and percentage of seropositive opossums were analyzed by the Spearman coefficient of rank correlation as outlined by Gibbons (1976: 274-284). The resulting coefficient was -0.05. This coefficient is very close to 0, and it indicates an almost total lack of association either positive or negative between capture rate and percentage of seropositive opossums.

A similar analysis of capture rate data and serum analysis data among cats during 1975 was performed. In this test the cat data from the 48 trap areas (Appendix L, Table 70) were put into four sets of 12 areas each. The Spearman coefficient of rank correlation was +0.40 which suggests that rabies seropositive cats were more common in areas with a high capture rate among cats, but this coefficient was not significant (P = .375).

In a final test the total data for the 1973-1976 period on opossum capture rates at roadside sides (Table 23, page 106) and the percentages of rabies seropositive opossums were considered. For this test the trap areas were grouped into 12 sets of four areas each. The Spearman coefficient of rank correlation was -0.03. This coefficient also reflects a distinct lack of any association between opossum capture rates and the percentages of rabies seropositive opossums among the trap areas. These data suggest that high population densities among opossums, as expressed by the capture rate, were not factors in the presence or absence of rabies seropositive animals.

The data summary for trap areas 1-24 suggests that
the rabies virus was present in many trap areas which did not
7 contain any reported rabies cases (Fig. 37). From 1972
through 1976 reported rabies cases occurred in 21 percent
(5/24) of the trap areas, but rabies seropositive animals
were found, over the 1973-1975 period, in 83 percent (20/24)
of the areas. Rabies seropositive animals were found in all

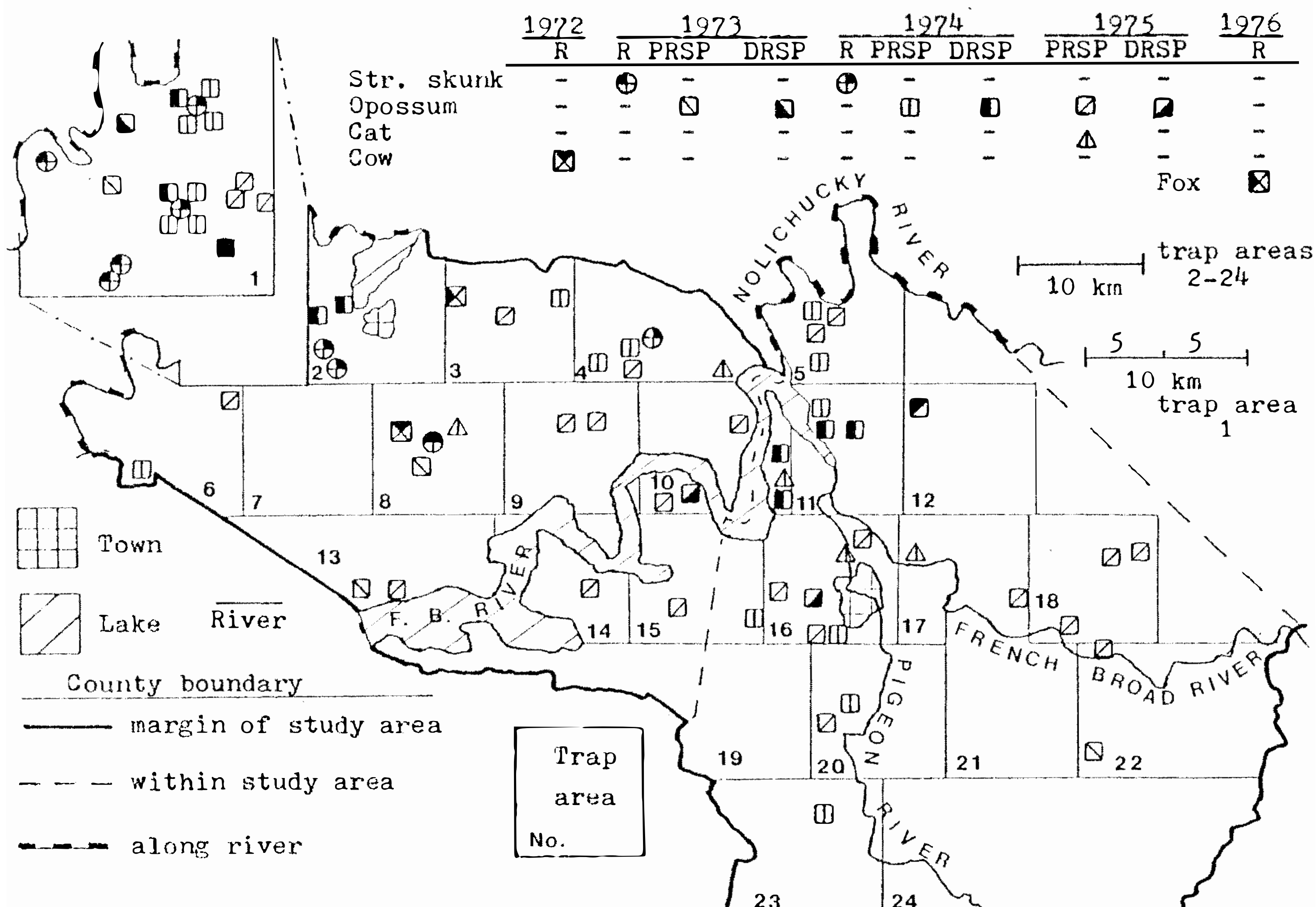


Fig. 37. Data summary for trap areas 1-24 showing the location of rabid animals (R), 1972-1976; presumptive rabies seropositive (PRSP) and definitive rabies seropositve (DRSP) animals, 1973-1976.

five of the trap areas with reported rabies cases.

Among trap areas 1-24 DRSP opossums were found in five trap areas (1, 2, 10, 11, and 16). These five trap areas appeared to form two foci of DRSP opossums. In one focal area, trap areas 1 and 2, the percentage of all rabies seropositive animals among animals captured at roadside sites was 26 percent (8/31) over the 1973-1976 period. Rabies seropositive animals were found in this unit of two trap areas each year during the 1973-1975 period. This focal area was closely associated geographically with reported rabies cases among striped skunks and adjacent to the site of the rabid gray fox. Seven of the 11 reported rabies cases from the 1972-1976 period in trap areas 1-24 occurred in either trap area 1 or 2.

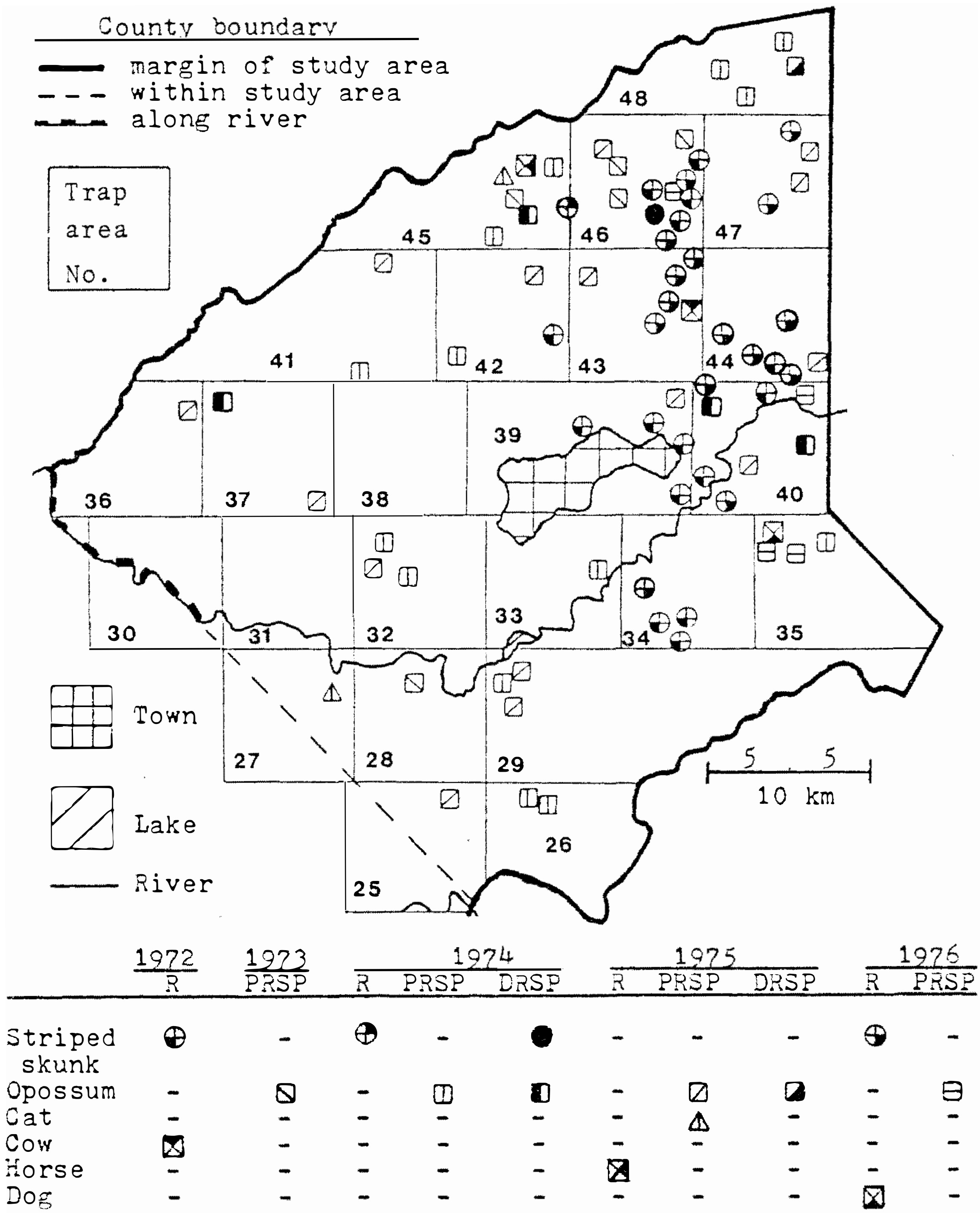
The other apparent focal area of DRSP opossums existed along the major rivers in trap areas 10, 11, and 16. In contrast to the situation found in trap areas 1 and 2, this focal area was entirely free of reported rabies cases during the 1972-1976 period, and the parts of this focal area in Cocke County existed in a county which had been free of any reported rabies cases since 1967. Along the Pigeon and French Broad rivers in these three trap areas, six DRSP opossums were captured. Expanding this area slightly to include the riverine sections of trap areas 4 and 17 would produce an area containing four of the seven PRSP cats collected in the entire study area. PRSP opossums were found along the three rivers flowing into this focal area and along the enlarged section of the French Broad River downstream. Three PRSP opossums were located in trap area 5 near the Nolichucky River flowing in from the north. The three PRSP opossums in trap areas 20 and 23 were captured near the Pigeon River as it flowed north toward the focal area. Four of the seven PRSP animals in trap areas 22, 18, and 17 were captured near the French Broad River as it flowed northwest. Downriver from the concentration of DRSP opossums, PSRP opossums occurred near the expanded French Broad River, Douglas Lake, in trap areas 15, 14, and 13.

Aside from the two major focal areas of rabies seropositive animals in trap areas 1-24, there seemed to be two small localized foci in Jefferson County. In the southwestern part of trap area 4 the rabid striped skunk of June 1974 was located near the sites of three PRSP opossums. In the center of trap area 8 another small focus occurred. Within a relatively small area there was a rabid cow (1972), a PRSP opossum (1973), a rabid striped skunk (1974), and a PRSP domestic cat (1975).

The aggregated data from trap areas 1-24 suggest that two major focal areas of DRSP animals existed for a time during the study in this part of the study area. One focal area was associated with reported rabies cases; the other was entirely free of reported rabies cases. Both foci were near major lakes or rivers. In southern Jefferson County and Cocke County most of the rabies seropositive animals were located near the major lakes and rivers.

3 The data summary for trap areas 25-48 (Fig. 38) shows that rabies seropositive animals were collected in 83 percent (20/24) of the trap areas, the same percentage found among trap areas 1-24. Of the 41 reported rabies cases in Greene County during the 1972-1976 period, the locations of 35 cases were determined, and these 35 cases were limited to 10 trap areas in the eastern and northeastern parts of the county. Four of the six DRSP animals (five opossums and one striped skunk) collected in Greene County were located in trap areas with reported rabies cases. One DRSP opossum was located in trap area 48 which was just north-northeast of a large number of reported rabies cases, and one DRSP opossum was found in trap area 37. The latter opossum was over 20 km from the nearest reported rabies case. Nine of the 10 trap areas with reported rabies cases contained at least one rabies seropositive animal. Trap area 34 was unique in that four rabid striped skunks were reported from the area, but none of the eight animals (six opossums and two cats) sampled in the area were rabies seropositive.

The overall pattern of rabies seropositive animals in trap areas 25-48 was not that of several distinct foci as seen in trap areas 1-24, but rabies seropositive animals apparently existed over much of the northeastern third of Greene County. The areas to the southwest of this extensive



Contiguous symbols represent animals at the same site

Fig. 38. Data summary for trap areas 25-48 showing the location of rabid animals (R), 1972-1976, presumptive rabies seropositive (PRSP) and definitive rabies seropositive (DRSP) animals, 1973-1976.

concentration of rabies seropositive animals appeared to contain very few seropositive animals, and the four trap areas (36, 30, 27, and 25) along the Greene-Cocke County boundary had only three rabies seropositive animals among the 50 tested.

In contrast to the association observed in trap areas 1-24, the majority of rabies seropositive animals in trap areas 25-48 did not appear along the major river of Greene County. While the six PRSP animals in trap areas 27, 28, 29, and 33 were near the Nolichucky River, the bulk of rabies seropositive animals were in the northern part of the county some distance from this river.

Aside from trap area 29 where two of the five animals tested were PRSP, the highest percentages of rabies seropositive animals were found in trap areas 45 (31 percent) and 46 (25 percent). As previously noted this two trap area unit contained some of the earliest, or only, reported rabies cases of the year in Greene County over the 1972-1976 period. Considering these two trap areas as a single unit, at least one rabies seropositive animal was found in this part of the county during each year of the serum survey. These data suggest that the rabies virus may have had an uninterrupted circulation among the animals of this region of the study area. This circulation apparently continued in the absence of reported rabies cases. During 1973 Greene County was free of reported rabies cases, but 50 percent (4/8) of the opossums in trap areas 45-46 were rabies seropositive, including one subadult.

An important aspect of the serum survey data was the determination of whether the distribution pattern of rabies seropositive animals had the strongest association with the pattern of past (retrospective), present (concurrent), or future (prospective) reported rabies cases. This aspect was considered by an analysis with the point correlation coefficient (Table 46). All the calculated average coefficients were positive except for the value based on the distribution of seropositive animals with rabies cases reported two years earlier, the retrospective coefficient (two years). The other four calculated average coefficients were positive, and the highest average correlation was +0.241 for the geographical association of rabies seropositive animals in a given year with the reported rabies cases in the following year, designated as the prospective coefficient (one year). The single highest correlation coefficient was between the rabies seropositive animals found during 1973 and the reported rabies cases during 1974. Reported rabies cases during 1974 occurred in three (trap areas 1, 8, and 45) of the seven trap areas with rabies seropositive opossums captured in 1973. One reported rabies case occurred in trap area 4 which was not a part of the 1973 survey. Rabies seropositive opossums from 1973 occurred in the absence of reported rabies cases during 1974 in trap areas 13, 22, 28, and 46.

Table 46. The relationship between the presence of seropositive animals (all species, both seropositive categories) and the current, future (prospective), and past (retrospective) occurrence of reported rabies cases.[a]

	Number of trap areas	Seropositive animals 1973	1974[b]	1975	Average value of analogous coefficients	
		7	21	34		
Rabid animals[c] 1972	8	+0.132	-0.056	+0.164		
Rabid animals 1973	2	+0.209	+0.026	-0.096	Retrospective coefficient (2 years)	-0.076
Rabid animals 1974	4	+0.516	+0.038	+0.193	Retrospective coefficient (1 year)	+0.117
Rabid animals 1975	1	+0.353	+0.165	+0.094	Concurrent coefficient	+0.114
Rabid animals 1976	8	-0.026	+0.056	+0.041	Prospective coefficient (1 year)	+0.241
					Prospective coefficient (2 years)	+0.204

[a]Relationship expressed as the point correlation coefficient (Fig. 8, page 51).

[b]Only animals collected in roadside trapping.

[c]Partial data, 18 of 24 cases.

The coefficients based on the 1973 serum survey data may be misleading. The sample size of the serum survey increased each year from 1973 through 1975, and as the sample size increased the number of trap areas with rabies seropositive animals also increased. The serum surveys for both 1973 and 1974 had the highest correlation coefficient with reported rabies cases during the following year. However, the 1975 serum survey had the largest sample size, 355 animals, and had the highest positive correlation coefficient with reported rabies cases in the preceding year, 1974. If a large sample size is considered to represent the true situation more accurately, then rabies seropositive animals may be more strongly associated geographically with areas from which rabid animals were reported in the preceding year.

Because of the variation among the sample sizes, it is not possible to determine whether the increasing number of trap areas which contained rabies seropositive animals over the 1973-1975 period reflected an actual expansion of rabies infection. The number of trap areas containing rabies seropositive animals did increase from seven in 1973, to 21 in 1974, and finally to 34 in 1975. Again, if the largest sample is taken as a more accurate reflection of the true situation, then the rabies virus was apparently distributed widely in the study area and was present in many areas with no reported rabies cases.

It is difficult to evaluate the data obtained during the serum survey as a means of predicting the areas where rabid animals might occur in the future. From 1972 through 1976 reported rabies cases occurred in an average of 4.6 trap areas per year, but during the 1973-1975 period rabies seropositive animals were found in an average of 20.7 trap areas per year. These data suggest that reported rabies cases, and perhaps all actual clinically rabid animals, occur in only a small portion of the areas with rabies seropositive animals. In some areas, as in trap area 34, reported rabies cases occurred where no rabies seropositive animals could be found. In general, the results of the serum surveys were not well suited for the precise determination of where future rabies cases might occur.

CHAPTER III

DISCUSSION

I. HISTORICAL TRENDS IN RABIES EPIZOOTIOLOGY

Rabies, as a clinical entity, is unique among wildlife diseases in that data are available on the species, location, and time of diseased animals over many years. Rabies is not a disease which achieves public recognition only during large epizootics, but a single case can have an important impact on a local area and thereby become part of the public health record. The aspects of species, place, and time are critical elements in the epizootiology of rabies, and a careful examination of the available data from reported cases can establish whether the epizootiology of rabies remained stable or changed with the passage of time. The extent to which rabies demonstrated a dynamic epizootiology in the study area and the larger study region was the first objective of this study.

Because the epizootiology of rabies over the years is based on reported case data, the validity of such data should be considered. The level of reported rabies cases in a given area may be influenced by the attitude of public health officials (Verts 1967:159) and the history of rabid animals (Parker 1962:278, Rakowski and Andrews 1972:70). While human population density may bias the reporting of any wildlife disease, some studies have suggested that the level of reported wildlife rabies cases is not completely dictated by this factor (Prior 1969:33-34, Schnurrenberger et al. 1970b:1338, Lewis 1972:247). Despite these uncertainties, data based on reported wildlife rabies cases constitute a framework for studying the major elements of rabies ecology (Wood 1954:132, Johnson 1966:25).

The three counties of the study area were considered in greatest detail, and the study accepted the idea that reported rabies cases were a reasonably accurate reflection of the true geographical extent and incidence level of the disease. The distribution of the human population within the study area did not appear to be responsible for the distribution of reported rabies cases. The personnel and procedures involved in rabies reporting did not appear to vary sufficiently to account for the disparity in the number and distribution of reported rabies cases among the counties of the study area. It is certain that some clinically rabid animals were not reported, but it did not appear likely that large numbers of clinically rabid animals existed undetected in areas some distance from the recognized clusters of reported rabies cases.

The argument for the general reliability of the rabies reporting system within the study area is supported by:

1. The long history of animal rabies in the area (Appendix H) has given the residents an awareness of the rabies problem.

2. The numerous small farms occupied by resident landowners create a situation which facilitates the observation of rabid animals.

3. The nature of work on a small farm which involves long hours of out-of-door activity also enhances the opportunity for observing rabid animals.

4. Pet dogs are extremely abundant and may serve to detect rabid wildlife. If such dogs are bitten, this exposure may form the basis for seeking a rabies diagnosis of both wild and domestic animals.

5. The presence of a free rabies diagnostic service which begins at the county level provides an easy means for confirming clinical rabies.

6. The aberrant behavior of clinically rabid animals may cause them to move into the living and working areas of study area residents.

The final point mentioned above may be considered in reference to the striped skunk, the major host among reported rabies cases during recent years. There is evidence to suggest that clinical rabies does not impair the mobility of striped skunks (Storm and Verts 1966:705). Furthermore, clinically rabid skunks may move aggressively toward a source of sound or movement (Verts 1967:168, Parker 1975:48). Therefore, clinically rabid skunks may be actively drawn toward isolated farm houses, barns, and kennel areas where the chances of human observation would be enhanced. These considerations suggest that the validity of the rabies reporting system in regions similar to the study area might be superior to many other reporting programs for wildlife diseases.

The study found that a high level of submissions for rabies diagnosis from a particular group of animals did not result in high numbers of positive rabies diagnoses. While the skunk was the major host of reported rabies cases during the 1972-1976 period in the study area, the number of skunk submissions (54) was exceeded by the number of submissions among dogs (123), cats (120), and foxes (68). Therefore, the dominance of skunks among reported rabies cases and the low number of reported rabies cases among dogs, cats, and foxes cannot be associated with the level of submissions among the groups. The number of animals submitted for a rabies diagnosis may have reflected the degree of contact which people had with that particular group of animals. Residents of the study area apparently had more contact with nonrabid dogs, cats, and foxes than with nonrabid skunks.

Many of the factors which contributed to the reliability of reported rabies cases in the study area may not have existed in other parts of the study region. While the study region did include counties in three states, the residents of the 30 counties undoubtedly share many social and economic practices. It is unlikely that any bias in the reporting system would allow Greene County to report 262 rabies cases from 1952 through 1976 while Mitchell and Jackson counties of North Carolina remained entirely free of reported rabies cases over these years, if, in fact, rabid animals were uniformly distributed within the study region. The study would suggest that such major disparities in the level of reported rabies cases reflected true differences in the presence of clinically rabid animals.

Starting from a qualified recognition of the value of reported rabies case data, the study examined the major patterns of rabies epizootiology. Among viral diseases such as rabies which have the capacity to infect a wide variety of species, the apparent dominance of one species or a closely related group of species such as foxes or skunks among clinical rabies cases has epizootiological significance. Furthermore, any changes in the major host species or the initial appearance of a new host species may reflect important epizootiological changes.

The most conspicuous trend in the reported rabies case data of the study region involved changes in the major rabies host species. Over a period of approximately three decades (1946-1976) the major rabies host was initially the dog, then the fox, and finally the skunk. This trend was noticeable for two counties of the study area and the study region as a whole.

Other reports have shown changes in the major host species of reported rabies cases. In the state of Florida the major rabies host was progressively the dog (1948-1955), the fox (1956-1958), and the raccoon in each year from 1959 through 1973 except 1965 when the bat was the largest single group of rabid animals (Prather et al. 1975:121). In Illinois the dog was the major rabies host from 1940 through 1956, and the skunk was the major host from 1957 through 1962 (Verts 1967:1959). In North Carolina the major rabies host was the dog (1952-1957), the fox (1958-1962, 1964, 1969), and the bat (1963, 1965-1968, 1970-1976). During 1976 the major host of reported rabies cases was the fox in Virginia, the skunk in Illinois, the raccoon in Florida, and the bat in North Carolina (USDHEW 1977:16).

There appeared to be three major changes in rabies epizootiology over the years considered. These changes were:

1. A shift from a period of dog rabies to a period of enzootic fox rabies in the late 1950's,

2. A shift from enzootic fox rabies to epizootic fox rabies in the mid-1960's,

3. A shift from epizootic fox rabies to a condition of periodic skunk rabies outbreaks in the early 1970's.

While these changes appeared to overlap when viewed in the regional rabies data (Fig. 9, page 58), the study area data (Fig. 15, page 77) show a gap of several years between the decline of dog rabies cases and the fox rabies epizootic with no period of enzootic fox rabies. Within the study area there was also a gap of approximately 21 months between the end of the fox rabies epizootic and the initial occurrence of reported rabies cases in skunks.

During the first major transition the decline in the incidence of dog rabies may be attributed to the systematic rabies vaccination of dogs which began in Tennessee during 1954. During the years when the dog was the major rabies host, the fox appeared to be only an incidental victim of rabies, perhaps as a result of chance encounters with rabid dogs. However, the regional rabies data indicate a substantial increase in fox rabies cases between 1956 (17 rabid foxes) and 1957 (65 rabid foxes). In the late 1950's the dog appeared to assume the role of an incidental rabies host, and the study region entered a period of enzootic fox rabies which was to last until the explosive fox rabies epizootic of 1964.

Two interesting aspects of this first transition and the subsequent period of enzootic fox rabies may be noted, but not explained. First, there was a noticeable decline in the number of counties which reported rabies cases (Table 11, page 59). The enzootic fox rabies condition was only evident in the counties of the northern part of the study region. Secondly, two of the three counties considered to be centers of dog rabies also became centers of fox rabies. These two counties, Lee and Scott counties of Virginia, form a continuous land area in the north-central part of the study region (Fig. 12, page 69). The latter consideration suggests that the conditions conducive to a persistent dog rabies problem may have been similar to those responsible for a persistence of rabies in foxes. However, these conditions could not be determined by the study. Furthermore, the extent to which the distribution of fox rabies cases was influenced by such fox population characteristics as density, nutritional status, and gene pool could not be determined.

The second major change in rabies epizootiology was the transition from enzootic fox rabies to the large fox rabies outbreak which began in 1964. There were three intriguing factors associated with this outbreak. First, the number of reported fox rabies cases declined noticeably for two years prior to the outbreak, and the level of fox rabies cases reported during 1963 was similar to that prior to the period of enzootic fox rabies (Table 10, page 55). Secondly, the epizootic during 1964 was most dramatic in Greene County which had not experienced a period of enzootic fox rabies. Thirdly, the initial cases of rabid bats were reported in the study region during 1963.

Considering these three points it is possible to speculate on the possible causes of the second major epizootiological change. The apparent decline of rabid foxes in the region during 1962-1963 may have produced an increase in the number of susceptible animals as a result of the reduced chance for exposure to rabies. The introduction of a rabid animal, such as a bat, into such a susceptible population may have triggered the rabies epizootic. Under laboratory conditions Constantine (1966:21-22) demonstrated that bats may infect foxes with rabies. Friend (1968:93) noted that the more dynamic rabies outbreaks occur in areas with the greater number of susceptible animals. The fact that reported fox rabies cases declined for two years prior to the outbreak may indicate that the epizootic was not the result of a fox population which had gradually reached a point of severe overpopulation. This predisposing factor might be expected to produce a more uniform increase in the level of reported cases. However, the fact that Greene County was south of the counties which experienced enzootic fox rabies forces the consideration of both (1) an increase in the proportion of susceptible foxes and/or (2) an increase in fox density to abnormally high levels.

Once the fox rabies epizootic began the disease appeared to move northeasterly up the valley portion of the study region (Fig. 14, page 72). The epizootic in a given county did not appear to develop any type of periodicity, but after several continuous months of fox rabies cases the incidence of the disease declined rapidly. The sudden decline in fox rabies cases as seen in the study area data (Fig. 15, page 77) may have resulted from less fox to fox transmission due to a drastic reduction in the fox population and/or an increased prevalence of rabies resistant foxes. Carey (1974:144-145) postulated that the proportion of rabies immune foxes in a population could influence the duration of interepizootic periods. Similarly, the presence of rabies immune foxes could result in the termination of a fox rabies epizootic.

Following the decline in reported fox rabies cases, the third major change in rabies epizootiology occurred. The skunk which had been only a very minor fraction of reported rabies cases became the major rabies host in the study region. The transition from the period characterized by fox rabies to the emergence of the skunk as the major rabies host may have resulted from an interspecific "spill-over" of rabies infection.

A theory to account for such a transition has been given by Sikes (1962:1046, 1966:32, 1970:9). He stated that skunks which are more resistant to rabies than foxes would be most likely to receive an infection sufficient to cause clinical rabies during periods when rabid foxes were numerous. Once the infection was established in skunks the high rabies virus titer in skunk saliva would kill those foxes bitten by skunks so rapidly that the disease would not become re-established among foxes by means of fox-to-fox transmission, but a skunk-to-skunk chain of infection would continue.

While it is possible that such a chain of events occurred in the study region during the late 1960's, the accumulated data of this study do not lend support to the theory of Sikes. These data involve facts relating the emergence of skunk rabies in relation to the major fox rabies outbreak of 1964-1967. The regional rabies data indicate that there was a distinct southward progression of skunk rabies cases which appeared to originate in the northern part of the region (Fig. 13, page 71). The available data point to Lee County, Virginia as the location of the earliest reported cases of skunk rabies. The presence of reported skunk rabies cases appeared to begin radiating southward from the Lee-Hancock County area during the early 1960's. This period was several years before the large fox rabies outbreak and a time of some decline in the number of reported fox rabies cases. Furthermore, the fox rabies outbreak during 1964 was most evident in the center of the study region, and several counties which reported large numbers of rabid foxes during the 1964-1967 period had not reported any rabid skunks by the end of 1967. For example, Greene County developed a persistent skunk rabies problem in the 1970's, but the county failed to report a single case of skunk rabies during the 1964-1967 period during which 185 rabid animals were reported among seven animal categories (Appendix H, Table 55).

If there was an interspecific "spill-over" of rabies infection, it probably occurred in the area of Lee-Hancock counties during a period of moderate but persistent fox rabies cases. While Lee County reported only the fifth largest number of fox rabies cases during the 1952-1976 period, the county had the most persistent record of rabid foxes and the largest number of years with reported rabies cases among all species within the 30 county study region (Table 13, page 66). Both Lee and Hancock counties were considered to be centers of fox rabies cases.

These data suggest that if rabid foxes were the source of rabies infection for skunks, the persistence of fox rabies cases over many years was more important in establishing rabies infections in the skunk population than very large numbers of rabid foxes during an epizootic of only one or two years. Furthermore, once the rabies virus began to produce clinical rabies in skunks, the occurrence of rabid skunks appeared to radiate into other areas without being noticeably influenced by the large fox rabies epizootic. This epizootiological pattern might suggest an intraspecific spread of rabies among skunks after the initial introduction of the disease into the population.

Several other epizootiological changes appeared to be associated with the transition of the skunk into the role of the major rabies host. While several counties in the north-central part of the study region were involved with wildlife rabies cases during both fox and skunk rabies periods, other counties in the northeastern and northwestern parts of the region did not experience an extended period of rabies among skunks. The basic geographical pattern among reported rabies cases which arose during the 1970's was a linear grouping of counties lying between the Cumberland Plateau to the northwest and the Appalachian Mountains to the southeast (Fig. 11, page 62). It is possible that these counties in the valley area of the study region provided better skunk habitat than the more mountainous areas to the northwest and southeast. In Illinois Verts (1967:79) noted that the highest populations of skunks were found in more open country, and the mountainous areas of the study region generally contain fewer areas of open land than the valley portion.

In addition to the change in spatial distribution, a major temporal change was also associated with the final epizootiological transition. Data from the study area and the study region suggest that little or no periodicity occurred among fox rabies cases. The fox rabies outbreak in each county of the study area was essentially a single, uninterrupted event (Fig. 16, page 78). This temporal pattern was reflected in the recurrence pattern of fox rabies cases within the study region during the 1957-1962 period when cases were often reported from the same counties year after year (Fig. 10, page 61; Table 12, page 64). However, after the decline of fox rabies cases, a periodicity among reported skunk rabies cases appeared. On the regional level skunk rabies upsurges were noted during 1969, 1972, and 1976 (Fig. 9, page 58; Fig. 22, page 125). The recurrence pattern among the counties with reported rabies cases during the 1971-1976 period indicated that rabid animals occurred in similar patterns after two and four years (Table 12, page 64).

A possible explanation for the difference in the temporal patterns of fox and skunk rabies could be based on the relative rabies resistance of the two groups of animals. Sikes and Tierkel (1962:271) indicated that skunks might be approximately 100 times more resistant to rabies than foxes. Therefore, rabies within a fox population might spread unabated from one fox to other foxes in an unbroken chain. However, among skunks the occurrence of some rabies resistant individuals, and perhaps the immune status of the entire population, might serve to periodically interrupt skunk-to-skunk transmission. The periodic skunk rabies outbreaks in the study region may have occurred when the number of susceptible skunks rose to a certain proportion of the population.

The overall impression taken from these historical data is that clinical rabies was not a static disease entity in the study region. Over the years considered, the distinct changes in species composition, geographical area, and periodicity of reported rabies cases suggest a dynamic relationship between the virus and the animals of the region. Regarding rabies cases among foxes and skunks, it is difficult to imagine that clinical rabies among these two groups occurred in similar proportions from the late 1950's through 1976, but that reporting biases initially favored the reporting of rabid foxes and later changed to the reporting of rabid skunks.

In considering the dynamic nature of rabies there should be a distinction between clinical rabies and rabies infection. It is conceivable that the extent of rabies infection among certain wildlife species changed very little, but a variety of factors may have dictated the appearance of the clinical disease in only one major group of animals during a particular period. These factors include (1) changes in the ecology of an inapparent rabies reservoir species, (2) mutations in the rabies virus, and (3) changes in the population and/or genetic characteristics of the visible rabies host species.

The historical trends seen among reported rabies cases do not appear to support the idea that an inapparent rabies reservoir species acted as the immediate source of rabies infection for the three major rabies hosts. It is conceivable that some members of such a rabies reservoir would, from time to time, develop clinical rabies and be exposed to detection by the residents of study region. Such potential reservoir species as the spotted skunk, mink (*Mustela vison*), long-tailed weasel (*Mustela frenata*), and several species of bats do exist in the area, but all except bats probably exist in low numbers relative to the combined abundance of opossums and cats. The serum survey results among opossums and cats (Table 45, page 194) suggest that these animals had considerable contact with the source of rabies infection. The available data during the 1972-1976 period in the study area also suggest that few clinical rabies cases developed in animals other than striped skunks and the domestic animals which may have been bitten by such skunks. Therefore, it seems unlikely that the rabies virus was maintained by such inapparent rabies hosts as the species mentioned above.

Other considerations also argue against the idea of an inapparent rabies reservoir species. The fact that noticeable geographical and, in some cases, temporal changes appeared to accompany the transition of the major rabies host would suggest that the occurrence of the disease was not the result of the direct transfer of the virus from such an inapparent host to the three major visible hosts (dogs, foxes, and skunks). However, it is conceivable that some inapparent reservoir of the disease persisted unaltered within the study region, and that radical changes in the population characteristics of the visible host species brought about the major transitions in the epizootiology of rabies as seen in the reported rabies case data.

The present study was not able to evaluate the role of population changes among the major rabies host species in the study region as a factor in the major transitions among host species. After evaluating commercial fur pelt data for Tennessee, Warren (1975:26-27) noted that gray fox populations were showing a gradual increase and red fox numbers were stable or increasing. The striped skunk population in the state appeared to be declining (Warren 1975:26). Therefore, the decline in fox rabies cases and the increase of skunk rabies cases in the state during the 1970's (Table 1, page 5) may not have been directly related to low numbers of foxes or high numbers of skunks. While local conditions may vary considerably from the overall pattern, these data are not consistent with the characterization of wildlife rabies as a density-dependent phenomenon as indicated by Marx and Swink (1963:170-171) and Toma and Andral (1977:20).

It is conceivable that the rabies virus experienced an antigenic shift prior to the major changes in major host species. Such antigenic shifts may be analogous to changes observed in the influenza virus which may have resulted from genetic recombination between human and animal influenza A virus (Fenner and White 1976:212-213). Fenner and White (1976:213) also noted that the emergence of a new influenza strain rapidly and completely displaced the preceding strain. Therefore, it is possible, from a virology perspective, that genetic recombination among differing strains of the rabies virus produced the major changes in the dominant rabies host species.

Other evolutionary changes may also have influenced the major transitions in rabies epizootiology. It is possible to speculate that high levels of clinical rabies among foxes over several years created evolutionary pressures which resulted in the selection of rabies resistant foxes. Data from the myxomatosis outbreak among rabbits in Australia suggest that selection for genetically resistant animals might operate rapidly (Fenner and White 1976:208). This selection could have created selective pressures on the rabies virus which resulted in a virus adapted to skunks. The apparent emergence of skunk rabies in those counties with a persistent fox rabies problem is in accord with this concept.

The major result of this analysis is the characterization of rabies as a dynamic disease entity. While the study can only speculate on the forces which produced the several epizootiological transitions noted in the region, an important public health implication may be suggested. If the epizootiology of rabies is not static, then the control measures which succeed during one period may not be applicable in latter years. The control measures used to control dog rabies may not be appropriate for the control of fox rabies, and the measures used to control fox rabies may not be suited to the control of rabies in skunks. The causative factors and public health implications of the major transitions in the epizootiology of rabies certainly merit further study.

II. GEOGRAPHICAL PATTERNS AND LANDSCAPE EPIZOOTIOLOGY REPORTED RABIES CASES, 1972-1976

While rabies data from the study region provided information on the broad geographical trends in rabies epizootiology, an examination of data on recent reported rabies cases within the three counties of the study area permitted a more detailed analysis of the distribution of rabid animals in space. This examination covered the five years from 1972 through 1976, and it was completely within the period dominated by rabies among skunks. Rabid skunks did, in fact, constitute 90 percent (47/52) of the reported rabies cases during these five years. The identification and interpretation of the geographical patterns among reported rabies cases constituted the second objective of the study.

Data from other studies have not produced a clearly defined spatial pattern for wildlife rabies cases. On a study area in northwestern Illinois, Verts (1967:167) noted that rabies infections in skunks may become established more or less simultaneously in several local areas. Rabies data from North Dakota were not sufficient to determine whether foci of rabid animals existed (Rakowski and Andrews 1972:70). Davis and Wood (1959:117) stated that fox rabies cases in the southeastern United States may occur at a high prevalence in a few small areas. However, fox rabies cases in Illinois between 1963 and 1968 did not show any geographical grouping

(Schnurrenberger et al. 1970a:1334). Rabies among Florida raccoons seems to occur in relatively localized epizootics (Bigler et al. 1973:327).

The data from the present study show that reported rabies cases were not randomly dispersed within the study area. On the county level the data revealed that only two of the three counties contained reported rabies cases during the 1972-1976 period. In spite of the fact that 89 animals were submitted for rabies diagnosis from Cocke County over these years, the county was free of reported rabies cases (Appendix H). This broad geographical pattern of rabies cases in the study area may have resulted from differences in wildlife populations, environmental factors, or a combination of many variables. However, this pattern may be related to the hypothesis that rabies infection among skunks originated in the northern part of the study region and progressed southward toward the study area. Within the study area the earliest rabid skunks were reported in Greene County during the spring of 1969, approximately two years after the last rabid fox was reported in that county. Greene County does extend farther north than either Jefferson or Cocke counties (Fig. 1, page 11). Rabid skunks were reported next in Jefferson County during 1973, approximately six years after the last reported case of fox rabies which could be associated with the large fox rabies epizootic of the mid-1960's. Jefferson County is adjacent to the northern part of Cocke

County. However, Cocke County is, to some extent, shielded from the north by major rivers (Fig. 2, page 13). The enlarged section of the French Broad River behind Douglas Dam flows between the western part of Cocke County and the northern part of Jefferson County. The Nolichucky River flows between the eastern part of Cocke County and much of the north and east of Greene County, and this river also forms the northern boundary of Cocke County. There were reported cases of dog rabies in Cocke County during the late 1940's and early 1950's. The county also experienced an outbreak of fox rabies during the mid-1960's. Therefore, the rabies virus has, at times, been present in Cocke County. The absence of any reported rabies cases among skunks in Cocke County may have been the result of restrictions in animal movement into the county from the north caused by these major rivers. Jennings et al. (1960:176) noted that major streams formed barriers to the progression of a fox rabies epizootic in northern Florida, and in some instances the epizootic failed to move across a river, but moved around the headwater of the river.

On a smaller scale two relatively small sections of the study area served as the location for the earliest or only reported rabies cases in each of the five years considered. These two areas were considered to represent microfoci of rabies infection. While these two microfoci were similar in geographical size, they varied in duration. In northwestern

Jefferson County, trap areas 1 and 2 represented a microfocus of clinical rabies in striped skunks which arose in 1973, existed through the spring and summer of 1974, and apparently disappeared after 1974. A second microfocus was considered to exist in trap areas 45 and 46. Considered together, these two areas contained some of the earliest reported rabies cases during 1972 and 1976, and the only reported rabies case in Greene County during 1974 and 1975. The rabies microfocus in northern Greene County apparently existed over at least five years. The microfocus of reported rabies cases in northwestern Jefferson County may have represented a temporary association of the factors responsible for clinical rabies among skunks, while the microfocus in northern Greene County may have been a more stable, persistent association of these factors.

The relatively long-term focal area in northern Greene County provided the best opportunity to discuss the implications of a microfocus of clinical rabies cases. Greene County was free of reported rabies cases from mid-August 1972 until May 1974, a period of approximately 20 months. However, considering trap areas 45-46 as a unit, half (4/8) of the opossums captured in these areas during 1973 were rabies seropositive. Some rabies seropositive animals were captured in these areas during 1974 and 1975 (Table 45, page 194). The serum survey data from 1973 suggest that the rabies virus was circulated in this focal area during part of the 20-month absence of reported rabies cases. Overall, the serum survey data suggest that (1) the rabies virus did not disappear from northern Greene County during the three-year inter-epizootic period of 1973-1975 and (2) the upsurge of reported skunk rabies cases during 1976 was not the result of a new introduction of the virus into the area.

Some rabies cases were reported outside of the two recognized microfoci. In Jefferson County reported rabies cases occurred in trap areas 3, 4, and 8. These cases occurred in either June, September, or December, and they may have represented the spread of rabies infection from the focal area in trap areas 1 and 2. In Greene County the spring rabies cases of 1972 and 1976 appeared over a broad area of the northern and eastern parts of the county within a relatively short period of time. While the early rabies cases and all reported rabies cases in Greene County during 1972 and 1976 were remarkably similar in geographical distribution, the available data are not sufficient to determine conclusively whether the rabid animals outside trap areas 45 and 46 resulted from a radiation of rabies infection from the single microfocus. If the rabid animals reported during 1972 and 1976 did represent the spread of rabies infection from such a focal area as trap areas 45-46, the dissemination was not uniform in all directions, but southward over the north-eastern third of Greene County.

Schwabe et al. (1977:14-16) stated that the major determinants of disease in populations are the disease agent, the host population, and the environment. The geographical characteristics of any disease are controlled by the spatial overlap of these three major determinants. The persistence of focal areas of rabies infection, if they existed, and the overall distribution of clinically rabid animals may have been influenced by one or a combination of these three determinants.

The geographical distribution of the disease agent, the rabies virus, did not appear to be the controlling factor in the distribution of reported rabies cases in the study area. The results of the serum survey strongly suggest that the rabies virus was present in many trap areas which were not associated with reported rabies cases (Fig. 37, page 199; Fig. 38, page 203).

Similarly, the distribution of clinically rabid skunks did not appear to be a function of the distribution of skunks in the study area. The available data on striped skunks located independently of reported rabies cases suggest that the species occurred in several trap areas which were free of reported rabies cases (Fig. 25, page 139). Most of the trap areas with striped skunks not associated with reported rabies cases also contained one or more rabies seropositive animals. These data suggest that striped skunks and the rabies virus coexisted in some parts of the study area which were free of reported rabies cases.

The logical extension of the preceding considerations is that the geographical distribution of clinical rabies cases among skunks in the study area was a function of the remaining major disease determinant, the environment. Those trap areas where clinically rabid animals were discovered may have contained some environmental feature or environmental complex not found in other parts of the study area. The environment could have exerted an influence on the virus-host system in a variety of ways, many of which could have been extremely indirect. The attempts to explain the geographical distribution of clinically rabid animals which appear concentrated in space constitute efforts to elucidate the landscape epizootiology of the disease. Many of the principles used in discussing the landscape epizootiology of rabies are found in the work of Pavlovsky (1966) who proposed the concept of the natural nidality of transmissible diseases in 1939.

The statistical examination of selected environmental features in relation to reported rabies cases and the skunks not associated with reported rabies cases indicated two geographical differences among these two groups of animals. First, some reported rabies cases appeared to be located farther away from the major river systems of the study area than skunks not associated with rabies cases (Table 29, page 136). This statistical association resulted primarily from the concentration of reported rabies cases in northern Greene County, and it should be noted that most of the reported rabies cases in northwestern Jefferson County were close to the Holston River. The second environmental difference was in the degree of forest/woodland cover in areas associated with these two groups of animals (Table 30, page 141). This second difference suggested that the skunks not associated with reported rabies cases occurred primarily in those trap areas with low to moderate forest/woodland cover while reported cases of clinical rabies were located primarily in the most open areas, the earlier reported cases, or in the areas with more than moderate cover, the later reported cases (Fig. 26, page 145).

Due to the meager data available on the distribution and abundance of striped skunks within the study area, it was impossible to determine conclusively the factors which dictated the geographical distribution of clinically rabid skunks. In general, however, there are three possible hypotheses to explain the spatial character of reported rabies cases. These hypotheses are that those areas with reported rabies cases were (1) areas of preferred or exclusively habitat for an inapparent rabies reservoir species, (2) areas of preferred striped skunk habitat which were capable of supporting high densities of striped skunks, and/or (3) areas of unsuitable striped skunk habitat which created certain stresses. The stresses associated with suboptimal habitat could reduce the ability of skunks to resist rabies infection. Stress may result in an increased output of corticosteroids which may exacerbate an otherwise trivial infection (Fenner and White 1976:132-134).

The study was unable to establish or reject the concept that the focal areas of reported rabies cases were the preferred or unique habitat of an inapparent rabies reservoir species. The lack of association between rabid animals and recognized caves does not support the idea that cave-dwelling bats serve as a rabies source for terrestrial wildlife. Mahan (1973:100-101) concluded that "there was no significant correlation between reported incidence of fox rabies and the percentage of bats positive for rabies virus" during his study in Tennessee. These data on wildlife rabies in Tennessee do not support the considerations of Fischman (1976) who suggested that rabies among foxes may be geographically associated with the distribution of caves and the bats which may inhabit these caves.

The second major consideration regarding the landscape epizootiology of rabies was that the areas with a high rabies incidence provided preferred habitat for the major visible rabies host, the striped skunk. In this case, the link between habitat and clinical skunk rabies cases would include population density and/or the longevity of individual skunks. If clinical rabies is a slow viral infection as suggested by Debbie (1974:241) and Gajdusek (1977:947), then the clinical disease might only appear several years after the initial infection. Since most striped skunks have a maximum life span of one or two years in the wild (Verts 1967:116, Linduduska 1947:128, Stout and Soneshine 1974b:143, Baily 1971:200), clinical rabies, when considered as a slow viral infection, would be limited to those areas where the host animals had an extended life span. This hypothesis suggests that rabies infections may be quite common and widespread, but most rabies infected animals would die of other causes before the symptoms of clinical rabies became evident. Transmission of the virus in the absence of clinical disease would occur in one or several of the nonbite transmission modes such as aerosol, urinary, venereal, neonatal infection of the young by their mother, or carrion feeding. The possible role of carrion feeding as a means of rabies transmission is considered in Appendix Q.

Presumably, the areas allowing for an increased longevity of skunks would be those areas of suitable or preferred skunk habitat. The more open areas of the study area, areas where most of the early rabies cases were reported (Table 30, page 141), may provide highly suitable skunk habitat which might, in turn, allow for increased longevity and/or higher population densities. Scott and Selko (1939: 96) noted that land use was important in relation to the population of striped skunks and noted that areas with hay and pasture land provided the most suitable den sites. Storm (1972:44) noted that Illinois striped skunks preferred certain habitats and avoided others. Verts (1967:79) found that the highest populations of striped skunks in northwestern Illinois were in the more open country. While the more open areas of the study area may have been preferred striped skunk habitat, the almost total lack of skunk captures in the trap areas or the farms associated with reported rabies cases suggests that skunk populations were not higher near the sites of clinically rabid animals. Overall, the relative merit of the second concept regarding the landscape epizootiology of rabies could not be determined.

The third concept related to the landscape epizootiology of rabies suggests that the areas with clinically rabid animals contained habitat which was unsuitable or suboptimal for skunks. The preferred habitat of striped skunks in the study areas may have occurred in those areas of mixed fields and woods exemplified in the study by a forest/woodland cover index from 0.7 to 1.1, the 12 trap areas of Groups 2 and 3 (Table 30, page 141). Fifty-three percent (9/17) of the striped skunks not associated with reported rabies cases were located in these 12 trap areas of low to moderate forest/woodland cover. While Verts (1967:79) did find the highest striped skunk populations in the more open areas, he did note that woodlots could be extremely important as skunk habitat under certain conditions. If the 12 trap areas represented by Groups 2 and 3 contained preferred skunk habitat, then clinical rabies among skunks occurred predominantly in non-preferred habits which were, perhaps, less suited to fulfilling the ecological requirements of striped skunks.

The third concept of the landscape epizootiology of rabies would postulate that the rabies virus is maintained and circulated widely within the study area as the serum survey data suggest. The clustered pattern of clinical cases resulted from disease occurring in animals experiencing stress as a result of a suboptimal habitat. The occurrence of clinical rabies in skunks occupying suboptimal habitats could be influenced by several factors. Some skunks in these marginal habitats would be subject to malnutrition which would reduce the ability to resist clinical disease (Fenner and White 1976:132-133). These skunks would be forced to forage over wider areas to secure food and thereby risk exposure to more rabies sources. Suitably secure and well-insulated winter dens are a critical requirement for skunks (Shirer and Fitch 1970:494), and an area without an adequate number of such dens would be suboptimal in this respect. If good den sites were in short supply, some skunks might be forced into intra- or interspecific communal denning. Houseknecht (1971:40-41) stated that among striped skunks there was, seasonally, a high degree of inter- and intraspecific contact through the concurrent use of dens, and he added that contact in such a denning situation would allow for disease transmission. It is possible that the areas of high reported rabies cases were areas with few good den sites.

With the available data the relative value of each trap area as skunk habitat and the relative abundance of skunks throughout the study area cannot be determined. The rather consistent failure to capture skunks in any part of the study area suggests that the focal areas of reported rabies cases did not have a greater or lesser abundance of the major rabies host, the striped skunk. Similarly, it is not possible to determine the extent of movement by skunks among the areas which might have been more or less suitable. The fact that only one skunk was captured on the 10 farms where clinically rabid animals were located would suggest that large populations of skunks were not common in the vicinity of reported skunk rabies cases. The occurrence of a rabid skunk was often the only evidence of skunk inhabitation for several of the trap areas. If the areas where clinically rabid skunks were reported had low skunk populations, there may have been movement of skunks into these areas from areas with higher skunk population densities, perhaps from locations outside the study area. Some of the rabid skunks reported in the study area may have been immigrants to the locations where they were found with rabies. The role of skunk population density in the geographical distribution of skunk rabies cases could not be determined.

In summary, there are several important points to emphasize in regard to the geographical aspects of reported rabies cases in the study area. These points are:

1. Cocke County, the only county without any reported

rabies cases during the 1972-1976 period, was separated from those areas of the study area where most of the reported rabies cases occurred by major rivers. These rivers may have served as a barrier to the introduction of clinically rabid animals into the county.

2. Within each of the two counties with reported rabies cases the earliest or only reported rabies case(s) of each year occurred within a relatively localized area which may be designated as a microfocus of clinical rabies cases.

3. While these microfoci were unique in the presence of early reported rabies cases, they were not the only trap areas with high percentages of rabies seropositive animals or the only areas with evidence of striped skunk inhabitation.

4. These microfoci may have contained some environmental factor or factors conducive to the development of clinical rabies in skunks. However, the degree to which these areas were suitable or unsuitable as skunk habitat could not be determined.

5. The two microfoci appeared to vary in their duration. The microfocus in northwestern Jefferson County, a relatively open area near the Holston River, lasted approximately two years. The microfocus in northern Greene County, a relatively open area away from major rivers, lasted over the five years of the study.

6. There were no data to indicate whether striped skunks were more or less abundant in the areas of reported skunk rabies cases. There was an equal lack of data regarding the extent of movement by skunks into and out of these areas.

While the factors responsible for the geographical concentration of reported rabies cases are unknown, several rabies control measures may be suggested by the data from the present study. These measures are:

1. Public health officials should carefully record the locations of all reported rabies cases in order to determine whether microfoci of rabid animals exist in their area of responsibility.

2. If such focal areas exist, residents within these areas should be informed of the possible danger and encouraged to submit animals exhibiting aberrant behavior for a rabies diagnosis.

3. These focal areas, if they exist, should be monitored for any changes in the abundance of the major rabies host which might signal an impending outbreak.

4. Any rabies control measures aimed at preventing rabies outbreaks such as the distribution of an oral rabies vaccine might be concentrated in any microfoci for greater economy and effectiveness.

III. MONTHLY INCIDENCE PATTERN OF REPORTED RABIES CASES, 1972-1976

The data regarding the incidence of reported rabies cases among skunks by month show that a temporal focus of rabid skunks existed in the study area. Thirty-eight percent (18/47) of all skunk rabies cases during the 1972-1976 period were reported during March, and 72 percent (34/47) of all reported skunk rabies cases occurred during the March-June period (Fig. 20, page 91). In four of the five years between 1972 and 1976, the earliest or only reported rabies cases occurred during the months of March or April. The data on animals submitted for rabies diagnosis by month (Table 19, page 93) suggest that this temporal focus was not completely dictated by the level of submissions during these months of the year.

Other studies have also indicated that reported skunk rabies cases are most numerous from the months of late winter into the early summer (Parker 1962:276, Schnurrenberger et al. 1964:163, Verts 1967:162, Friend 1968:88). In North America fox rabies cases have been found to peak in late winter, usually from December to April (Friend 1968:82, Johnston and Beauregard 1969:358, 360, Prior 1969:26-28, Winkler 1975:19). If time is allowed for varying incubation periods, it would appear that many rabies infections are either acquired or reactivated during the months of late winter or early spring.

Within the study area several ecological factors could be responsible for the temporal focus of clinically rabid skunks. The rate of contact between skunks may increase during late winter due to such factors as communal denning and/or reproductive activity. Any increase in the rate of contact between skunks would increase the opportunity for direct rabies transmission. Houseknecht (1969:304-305) found evidence of considerable communal denning by striped skunks during the winter denning period and suggested that the activity within such winter dens could facilitate the direct transmission of disease. The annual breeding period of striped skunks occurs during late winter (Verts 1967: 106, Bailey 1971:198), and this intraspecific contact could also result in rabies transmission and the observed peak in rabid skunks during late winter-early spring. These considerations suggest that the temporal focus resulted from rabies infections acquired during late winter and that these infections progressed directly through the incubation period into the clinical disease.

While the preceding considerations provide a partial explanation for the temporal focus, other factors must be examined. The factors responsible for any temporal focus of an infectious disease are linked in some manner to the mechanisms whereby the disease agent is maintained and transmitted. The classical bite transmission of rabies was undoubtedly a factor in the dissemination of the virus, particularly during the late winter and early spring. However, even considering the variations possible in the incubation period, a tentative proposal of this study is that the rabies virus was not transmitted throughout the year by means of an unbroken chain of bite transmission from clinically rabid animals to other susceptible animals. Verts (1967:172) suggested that certain skunk population characteristics during interepizootic periods would present insurmountable obstacles to the perpetuation of rabies among skunks by means of bite transmission. The maintenance of rabies by means of a continuous series of bite transmissions would seem to necessitate a more uniform distribution of reported rabies cases during the year. Certainly, the chances of humans observing rabid animals would be greater in the summer months when there are more daylight hours and more outdoor activities by residents of the study area. Therefore, it is conceivable that some form of biological reservoir mechanism maintained the rabies virus in a subclinical relationship with the animals of the areas during the late summer to early winter period, and that this mechanism was disrupted during the late winter.

As an alternative to direct bite transmission of rabies, the temporal focus could have resulted from the reactivation of long-term, latent rabies infections. Evidence suggesting the existence of latency in rabies infections is summarized by Bell (1975:333-334). Verts (1967:174) suggested that female striped skunks with latent rabies infections might transmit rabies to their offspring as latent infections. McLean (1975:74-75) suggested that latent rabies infections among raccoons were a conceivable type of biological reservoir mechanism, and he noted some support for the concept of sublethal rabies infections among Florida raccoons. The concept of a temporal focus of clinical rabies based upon the reactivation of latent infections rather than an unbroken series of short-term infections progressing directly to clinical disease is consistent with the noticeable lack of reported rabies cases in the study area during the fall and early winter which was apparent in each year except 1976.

If latent rabies infections do occur among striped skunks of the study area, the temporal focus may have resulted partially from the reactivation of these infections. Reactivation may have resulted from the physiologic changes during breeding activity and stress (McLean 1975:75). Verts (1967:175) stated environmental stress could reactivate latent rabies infections among striped skunks, and such stress could occur at different seasons for males and females.

In most of North America, winter and particularly late winter creates harsh environmental conditions for wildlife. Sunquist (1974:443) found that striped skunks may lose 49 to 58 percent of their fall body weight during winter. Verts (1967:123) noted that the loss of half of the prefasting body weight was possibly near the maximum if recovery was to occur. Houseknecht (1969:304) noted that many striped skunks may lose 55-65 percent of their fall weight during the winter denning period. Since skunks do not cache food in their dens (Sunquist 1974:444), starvation may be a mortality factor among skunks during the winter (Verts 1967: 123). The reduction in physical condition produced by inadequate nutrition can exacerbate any infection (Fenner and White 1976:132-133), and could, in theory, reactivate a latent rabies infection.

In addition to the preceding considerations, the study would propose a hypothesis to account for the temporal focus of skunk rabies cases in the study area. This hypothesis is based upon the dual concepts of latent rabies infections for the maintenance of the virus and carrion feeding as a mode of transmission. This hypothesis and its relationship to the temporal focus of clinical rabies cases are presented in detail in Appendix Q. The basic points of this hypothesis in relation to the temporal focus of clinical rabies cases are:

1. A variety of environmental factors would increase late winter mortality, particularly in suboptimal habitats (Verts 1967:123, Sunquist 1974:443-444).

2. Some of these dead animals would have had a rabies infection (Verts 1967:123, Burkel et al. 1970:499), and the cold temperatures would preserve infective viruses longer (Soave 1966:45, Burkel et al. 1970:497).

3. Surviving skunks faced with diminished fat reserves and few sources of plant food would rely more on carrion feeding to secure food (Hamilton 1936:245).

4. Skunks which fed on rabies infected carcasses could ingest rabies infected tissue and develop a rabies infection (Correa-Giron et al. 1970:206-207, Fischman and Schaeffer 1971:79, 84, Ramsden and Johnston 1975:320-323).

5. Some of these infections would progress directly through the incubation period and become the clinical rabies cases of the early spring with some bite transmission resulting in clinical rabies cases continuing into the summer.

6. Other rabies infections would remain subclinical, perhaps with the formation of serum antibodies, and these infections would provide a source of infection for the next late winter period.

At the present time there are no data to indicate conclusively which of the several theories mentioned may be responsible for the temporal focus of skunk rabies cases, or even that all possible theories have been included. However, several undertakings may be suggested for future research and rabies control. These include:

1. Greater efforts to collect and diagnose skunks for rabies during the late summer to mid-winter period in order to determine whether the temporal focus of clinical rabies cases during late winter actually exists.

2. Efforts to gather detailed biological data on the

rabid skunks of late winter and compare these data with a sample of skunks collected in the same area and diagnosed as nonrabid in order to determine any unique characteristics of skunks which develop clinical rabies.

3. The application of rabies control procedures such as the dissemination of oral rabies vaccine may be most effective if applied during the fall and early winter.

IV. REPORTED SKUNK RABIES CASES AND SKUNK POPULATION CHARACTERISTICS

During a period of enzootic rabies, it may be assumed that clinical rabies cases occur in only a segment of the host species population. If the biological parameters of this segment can be defined, significant insights may be developed into the epizootiology of the disease. In this regard three factors of the skunks not associated with reported rabies cases were evaluated in relation to similar data from skunks reported as clinical rabies cases. These factors were (1) sex, (2) age class, and (3) population dynamics.

The present study was unable to determine whether the sexual composition of clinically rabid skunks differed from that of skunks not associated with reported rabies cases. Verts (1967:172-173) noted a marked difference in the sexual composition among rabies infected skunks during different seasons of the year. In the present study the only two rabid skunks which were noted for sex were evenly divided with one male and one female. The study would recommend that the sex of all animals submitted for a rabies diagnosis be routinely recorded in order that this aspect of rabies ecology can be investigated.

On the basis of size the overwhelming majority of reported skunk rabies cases in the study area appeared to occur among adults (Appendix J). Considering that most reported skunk rabies cases occurred during the first six months of the year, the predominance of adults among rabid skunks is not surprising. In the study area young skunks from the single breeding season probably become independent during the middle or late summer months as reported by Verts (1967:40-41) in Illinois and Bailey (1971:199) in Ohio. Verts (1967:174) noted that if the adult female died of rabies before the young skunks were weaned, the young would probably die of starvation. Therefore, if young skunks received a rabies infection from a clinically rabid mother, they might die of parental neglect before developing clinical rabies or be unable to move over an area large enough to be detected by humans.

It is conceivable that the occurrence of clinically rabid skunks during the fall and early winter is dependent upon a sizeable recruitment of juveniles into the skunk population. Verts (1967:164) noted that 80 percent (36/45) of the rabid skunks submitted to the laboratories in Iowa and Illinois between September and December 1961 were less than 12 months of age. Webster et al. (1974:165) found that skunks which were less than one year of age constituted 63 percent of the skunk rabies cases in Ontario during December. Bailey (1971:201) reported that self-sufficient juvenile striped skunks were captured more frequently than adults during the period of July-September. Obviously, independent juvenile skunks would be most abundant during the fall, and the young-of-the-year might compose a large portion of the skunk population as winter approaches.

During the present study only 11 percent (5/46) of the skunk rabies cases in the study area were reported during the months from September through December, and these five cases all occurred during 1976. There were no data to indicate that a fall upsurge in skunk rabies cases was an integral part of skunk rabies ecology in the study area. One possible explanation for these data would be that the absence of skunk rabies cases during the fall resulted from low numbers of that segment of the host population, juveniles, which would normally constitute these cases. This hypothesis would suggest that skunk reproduction within the skunk area was quite low. The striped skunk population studied by Stout and Soneshine (1974b:143) in Virginia apparently had "low recruitment and/or survival" of young skunks and may have represented an unproductive skunk population. Within the study area there may have been a high juvenile mortality rate and/or a very small breeding population of striped skunks. There is some support for these suggestions in that (1) very few skunks were captured during the study (Table 22, page 102) and (2) on the basis of body size, only one of the 12 road-killed striped skunks observed in the study area appeared to be a juvenile (Table 27, page 122). If the resident skunk population of the study area was small, there may have been some immigration of skunks into the study area. Such immigration, if it existed, could have introduced rabies infected skunks into the area and/or added new susceptible skunks to the resident population. However, the meager data regarding the striped skunk population in northeastern Tennessee prevented any conclusive evaluation of these considerations.

Skunk population dynamics is the third aspect to be considered in relation to the incidence of skunk rabies cases. Other wildlife rabies studies have suggested that clinical rabies is a density dependent phenomenon (Rausch 1958:255, Marx and Swink 1963:171-172). However, much of the data indicating that rabies incidence is strongly density dependent comes from studies of fox rabies. Verts (1967:171) stated that "epizootics of rabies among striped skunks involve considerably more than a high population level of hosts over a wide area." As noted in the discussion on the historical rabies data, major differences seemed to exist between the epizootiological patterns of fox and skunk rabies. The major point to consider is that clinical rabies among foxes may be a density dependent, population regulating phenomenon, while the same disease among skunks may have entirely different causes and effects.

The available data for the state of Tennessee suggest that the number of skunk pelts collected by fur trappers declined drastically during the 1950's (Fig. 23, page 129). During this period the skunk was apparently an incidental victim of rabies (Table 1, page 5). By 1958 the number of skunk pelts sold by Tennessee trappers was less than 2,000 per year, and this level changed very little during the 1960's and early 1970's. The number of reported skunk rabies cases did not begin to increase until the early 1960's, several years after the skunk population appeared to have stabilized at the reduced level. The two large skunk rabies outbreaks which occurred during 1965 and 1972 were not associated with any noticeable change in the number of striped skunk pelts collected by trappers.

These data from Tennessee are remarkably similar to data given by Parker (1962:277) for four north-central states. Data from this paper also showed a major decline in the number of skunk pelts harvested by trappers from 1940 through the late 1940's while the skunk was only an incidental rabies host. Then several years after the decline reached a relatively stable low point, the incidence of reported skunk rabies cases began to increase dramatically.

The number of skunk pelts harvested from this region remained relatively stable through the 1960's while the level of reported skunk rabies cases fluctuated widely, a situation quite similar to the state-wide data for Tennessee.

The two major epizootiological implications of these state and multi-state data on skunk pelts harvests and reported skunk rabies cases are (1) the transition of the skunk from an incidental rabies host to a major rabies host appeared to follow a major decline in the population of skunks rather than a major increase in the skunk population and (2) once the skunk became an important rabies host the fluctuations in reported skunk rabies cases did not appear to parallel any noticeable fluctuations within the skunk population, as reflected by the number of skunk pelts harvested.

One possible interpretation of the first implication is that clinical rabies among skunks may rise drastically in skunk populations which are experiencing some environmental stress. Such factors as habitat destruction, a reduction in food supply, and/or increased parasitism and diseases other than rabies could reduce skunk populations, lower resistance to the rabies virus, and initiate an upsurge in clinical skunk rabies cases. The second point mentioned above suggests that any periodicity of skunk rabies cases over several years may be related to some factor other than changes in the density of the skunk population. Perhaps, changes in the ratio of immune and susceptible skunks, the herd immunity of the skunk population, influenced the periodicity of skunk rabies cases. Schwabe et al. (1977:159) noted that changes in herd immunity might be responsible for the two to three year cycle of canine distemper among urban dogs.

On a smaller scale the role of skunk population dynamics within the three-county study area on the incidence levels of skunk rabies cases was difficult to evaluate. The meager data from skunk captures and the low number of observed road-killed skunks suggest that skunks were not abundant during any year of the study. For this reason the special six county area served by a Hamblen County fur buyer was considered (Fig. 22, page 125). The data on the number of skunk pelts purchased by this dealer and the number of reported skunk rabies cases in the six counties reinforced several of the trends seen on the state level. These major trends from this area in northeastern Tennessee were:

1. Based on a decline in the skunk pelts sold by trappers, the initial upsurge in skunk rabies cases appeared to occur after the skunk population had been in decline for several years.

2. Reported skunk rabies cases began a periodicity with peaks separated by three or four years.

3. The number of skunk pelts collected by trappers were not unusually high prior to the periodic skunk rabies upsurges, but the absence of rabid skunks may have been related to extremely low skunk population levels.

The first trend mentioned above may provide a clue to an earlier observation concerning the regional spread of skunk rabies cases. It was noted that the initial appearance of rabid skunks seemed to move southward into the study area (Fig. 13, page 71). It is possible to speculate that the decline in the skunk population of northeastern Tennessee, suggested by the decline in skunk pelts harvested, created an area of low skunk density which attracted other skunks into the area. In reference to areas of low fox density following a fox rabies epizootic Sikes (1970:10) stated:

> Assuming that the food supply and other factors necessary to support a stable population of the species still persist, the population vacuum can be expected to be filled by animals from contiguous, unaffected areas and the offspring of the few animals that survive the infection.

If such a low density area, or vacuum, created an influx of skunks from the north where clinical rabies among skunks was first reported, then a southward progression of skunk rabies cases would appear logical. The present study agrees with the opinion of Warren (1974:26) that the declining number of striped skunk pelts collected by Tennessee trappers signified that "skunk populations appear to be declining." Several residents of the study area expressed the opinion that skunks were not as common as they once were. Unfortunately, no explanation is currently available to account for the apparent decline in the skunk population of northeastern Tennessee or the state as a whole.

The second and third trends mentioned above suggest that the apparent upsurges of reported skunk rabies cases were separated by three or four years, and these peaks did not appear to be density dependent phenomena in the sense that increasing rabies mortality occurred as the skunk population increased. However, the data from Fig. 22 (page 125) suggest that the absence of reported skunk rabies cases may have resulted from extremely low number of skunks in the area. During the 1974-1975 trapping season no skunk pelts were bought by the Hamblen County fur dealer, and no rabid skunks were reported in the six county unit during 1975. In considering the recent skunk rabies data from Greene County, it was noted that a strict two-year cycle for skunk rabies upsurges would have produced an upsurge during 1974. The absence of such an outbreak may have resulted from a low population level of skunks as reflected by a declining skunk pelt harvest from the 1972-1973 season to the 1974-1975 season in the six county unit and the low capture rate of skunks within Greene County.

If the periodicity of skunk rabies upsurges was not the result of fluctuations in skunk population density, then alternative factors should be suggested. The serum survey data suggest that the rabies virus appeared to persist within the study area between the upsurges of reported rabies cases. Therefore, a periodic reintroduction of the disease agent did not seem responsible for the periodic outbreaks of clinical rabies cases. Two other phenomena may be considered to account for these data. These phenomena are (1) periodic migrations of skunks into the areas where rabid skunks occurred and (2) changes in the immune status, herd immunity, of the resident skunk population.

Neither of these two concepts can be evaluated conclusively with the present data. It is possible that the rabies virus was circulated continuously within the study area, and that periodic influxes of small numbers of skunks into the focal areas resulted in the noticeable upsurges in reported skunk rabies cases. It is also conceivable that the focal areas did not experience such periodic influxes, and that these areas were continuously inhabited by a small skunk population. When the proportion of rabies susceptible skunks in this resident population reached a certain level, minor upsurges in the number of clinical rabies cases occurred. Sikes (1970:10) stated:

> When the ratio of susceptible to infected animals reaches the proper proportion, another rabies epizootic will occur. The disease status of an area may change from enzootic to epizootic according to these shifts of populations and ratios of infected to susceptible hosts.

An elaboration of the latter idea would suggest that during an outbreak of clinical rabies in skunks, the rabies virus was widely disseminated in such a manner as to produce a skunk population composed primarily of rabies immune animals. As noted in Appendix D, Table 50, the percentage of rabies seropositive skunks in natural populations has been found to range from 0 (Sikes 1962:1047) to over 50 percent (Niemeyer 1973:14). If the rabies immune status of a single skunk population varied over a similar range, such alterations over several years could very well influence the periodicity of skunk rabies outbreaks. This concept would suggest that as immune skunks died and were replaced by susceptible skunks through either reproduction or immigration, the potential for another upsurge of clinically rabid skunks would increase. Verts (1967:121) noted that striped skunks may have a short life span with less than 35 percent of young skunks reaching the age of one year. Linduska (1947:129) stated that only one of 115 captured striped skunks was known to have still been on a study area for more than two years after the initial capture. Therefore, a population of striped skunks might experience an almost complete turnover of members over a two or three year period, an interval similar to the periodicity of skunk rabies outbreaks.

In summary, the study would suggest several general associations between skunk populations and the incidence of clinical rabies in skunks. These associations are:

1. The transition of the skunk from an incidental rabies host to the major rabies host may have occurred in a skunk population experiencing major environmental stress. The initial increase in clinical rabies cases among skunks

appeared to occur in an area where the skunk population had apparently been in decline for several years.

2. The general absence of rabid skunks during the fall may have resulted from an absence of a large juvenile segment of the skunk population which may, in turn, have resulted from a small breeding population of skunks within the study area. This association may also have reflected a skunk population under environmental stress.

3. The level of clinically rabid skunks did not appear to be a density dependent phenomenon in the sense that skunk rabies outbreaks were dependent on abnormally high skunk population densities. The apparent periodicity of skunk rabies upsurges may have been related to changing proportions of rabies susceptible skunks in the population and/or periodic migrations of a limited number of skunks into the area. Neither of these two factors would necessarily alter dramatically the population level of skunks in the study area.

Because of the uncertainty associated with the population factors influencing the initiation and periodicity of skunk rabies cases, it is difficult to suggest any management procedures for controlling skunk rabies. If skunk rabies outbreaks are not dependent on high skunk population densities, then population reduction efforts may not be the best way of controlling clinical rabies among skunks. In fact, population reduction programs initiated after the peak of a skunk rabies epizootic may remove many skunks which might be rabies resistant. The removal of rabies resistant skunks might hasten the onset of another skunk rabies outbreak by increasing the rate at which susceptible skunks are added to the population. This concept was noted by Carey (1974: 144-145) in regard to rabies control among Virginia foxes. The application of a safe and effective oral vaccine might be productive, but the expense involved in such a program among short-lived animals may not be justifiable. Certainly, the roles of changing immune status and skunk movement patterns in relation to the periodicity of clinical rabies among skunks deserves further study.

V. EPIZOOTIOLOGICAL IMPLICATIONS OF THE SERUM SURVEY DATA

The serum survey among the animals in the study area sought to provide data unbiased by rabies reporting procedures on the rabies virus in regard to the range of species infected, geographical distribution, and persistence over the years. These data provided the basis for considering the fifth objective of the study.

The study determined that at least one member of the three species tested was rabies seropositive (Table 45, page 194). While the sample sizes varied greatly, rabies seropositive animals constituted 33 percent (1/3) of the striped skunks, 12 percent (5/57) of the free-roaming domestic cats, and 17 percent (101/608) of the opossums sampled in the study area. Among these three species clinical rabies cases were reported only in skunks, most, if not all, of which were striped skunks (Appendix J). One of the most important issues concerning these data involves the factors responsible for the diversity of species which apparently experienced rabies infections. Several of the most likely possibilities which may have occurred singularly or in combination involve:

1. A common exposure to an inapparent rabies vector species, a species not sampled during the study or among reported rabies cases during the study period.

2. Several independent, closed, species-specific transmission cycles whereby the rabies virus or a "strain" of the rabies virus was circulated solely by intraspecific contact.

3. A variety of interspecific transmission cycles with no single reservoir host or a reservoir host among the species sampled during the study.

At the present time the relative merits of these three alternatives cannot be established.

Within previous sections of this discussion, it was mentioned that no evidence was found to support the concept that an inapparent host species served to disseminate the rabies virus via individuals which were clinically rabid. Naturally, the possibility remains that the rabies virus was disseminated by such an inapparent host species which contained members with asymptomatic rabies infection but still capable of shedding the virus. This aspect of the rabies ecology in northeastern Tennessee must await the results of future research.

In regard to one of the many possible interspecific rabies transmission cycles, the study did not consider clinically rabid skunks as a likely source of rabies infection for opossums and domestic cats. This hypothesis is based on a number of findings from the data of the present study and data from other investigations.

Initially, it would be valuable to consider the possible extent of rabies exposure within the opossum population. While the study data revealed that approximately one sixth or 16.6 percent (101/608) of the opossums sampled were rabies seropositive, it is quite likely that the percentage of opossums which had been exposed to the rabies virus was much greater. Barr (1961:59-60) found that only 17.6 percent (3/17) of the opossums exposed to the rabies virus in his laboratory study developed detectable rabies antibodies. This percentage is remarkably similar to that found among opossums in the present field study. Theoretically, it may be postulated that only 18 percent of the opossums exposed to rabies actually develop a detectable rabies antibody titer. If this is the case, then an opossum population in which approximately 17 percent of the animals have rabies antibodies could indicate an almost universal dissemination of the rabies virus. The average percentage of rabies seropositive opossums within the four weight classes designated as adults, opossums weighing 1.4 kg or more, was 20 percent (Table 44, page 188). These considerations suggest that a large majority of adult opossums and a sizeable segment of the total opossum population may have been exposed to rabies.

It is doubtful that such widespread rabies circulation could have been achieved by bite transmission from clinically rabid skunks. This idea is supported by data regarding the abundance of skunks in relation to opossums and cats. During the study there were 793 opossum captures, 388 cat captures, and only three striped skunk captures (Table 28, page 131). Even with allowances for large sampling errors, there could have been 50 to 100 opossums for each striped skunk in the study area. Furthermore, clinically rabid skunks may have constituted a small segment of the total skunk population, and thus the number of opossums for each clinically rabid skunk in the study area would have been very large. Therefore, the ability of clinically rabid skunks to infect large numbers of opossums and cats over a large part of the study area seems unlikely.

In some parts of the study area the abundance of rabies seropositive animals without any reported rabies cases argues against clinically rabid animals as a source of rabies infection among opossums and cats. However, the possibility that unreported rabies cases, perhaps in large numbers, may have occurred in these areas must be considered. To address this point the northern part of Cocke County along the border with Jefferson County, particularly trap areas 10, 11, and 16, may be examined. Several factors tend to support the idea that if clinically rabid animals occurred in these areas, they were few in number. Trap area 16 contains the town of Newport, population 7,328 in 1970, which is the location of the Cocke County Health Department where animals may be submitted for a rabies examination. The concentration of the human population and the ready access to a rabies diagnostic service would seemingly enhance the probability of some rabies cases being reported if clinically rabid animals were present in large numbers. Trap areas 10 and 11 have an extensive shoreline with the enlarged portion of the French Broad River, also known as Douglas Lake. This shoreline is regularly used by local residents during the spring, summer, and fall for outdoor recreation. The use of this area as an outdoor recreational area would also appear to facilitate the reporting of some rabid animals if they occurred in large numbers. Therefore, it is possible to postulate that if clinically rabid animals existed in trap areas 10, 11, and 16, they were few in number.

This section of the study area designated by trap areas 10, 11, and 16 was selected for consideration because it appeared to represent a focus of rabies seropositive animals existing in the absence of any reported rabies cases. Over the entire study, 32 percent (15/47) of the combined number of cats and opossums sampled in these three trap areas were found to be rabies seropositive (Table 45, page 194). Such an abundance of rabies seropositive animals would suggest that the source of rabies infection in these areas was also quite abundant. However, if the idea that the northern border area between Cocke and Jefferson counties experienced few clinically rabid animals is accepted, then the hypothesis that clinically rabid animals were the source of rabies infection for opossums and cats does not seem feasible. It would seem extremely doubtful that the number of clinically rabid animals needed to infect, by biting, almost one third of a small sample of cats and opossums could have existed in this part of the study area without a single reported rabies case in any species. Cocke County was free of reported rabies cases from 1968 through 1976 in spite of the fact that 132 animals were submitted for rabies diagnosis (Appendix H, Table 54).

There is one final consideration on the ability of clinically rabid striped skunks to serve as the source of rabies infection among opossums and cats. It may be postulated that clinically rabid skunks are not effective disseminators of the rabies virus. Observations of clinically rabid skunks in the study area indicated that many of these animals were uncoordinated, lethargic, and nonaggressive (Appendix J). In reference to a striped skunk rabies outbreak in a laboratory environment, Gough and Niemeyer (1975:176) reported that:

> The epidemic of rabies in the skunk colony spread slowly although animals were in intimate contact with each other. Generally a rabid skunk infected only a single animal, if any at all (. . .). There was a low rate of transmission of rabies between animals in very close contact, most rabid skunks were not aggressive and the duration of illness of the animals in this epidemic was short.

The rabies virus responsible for this outbreak had been acquired through a natural infection, and most of the rabid skunks died without showing any clinical signs. In regard to bite transmission of rabies it is interesting to note that some skunks which die of clinical rabies never produce detectable levels of virus in their saliva. Data from laboratory studies have shown that the percentage of rabid skunks shedding the virus in their saliva was 83 percent (15/18) (Sikes 1962:1043-1045) and 75 percent (15/20) (Parker and Wilsnack 1966:37).

While rabies virus may be present in the saliva of rabid skunks several days before any clinical symptoms appear (Sikes 1962:1043-1044, Parker and Wilsnack 1966:37), other factors argue against the ability of even physically unimpaired skunks to infect by biting large numbers of opossums and cats. The striped skunk, even when healthy, is a relatively slow moving, semiplantigrade animal. Striped skunks are not climbers (Verts 1967:33), and they are not known to climb trees. Opossums and cats are excellent climbers and often seek safety in trees. These considerations would cast doubt on the ability of a clinically rabid skunk to overtake and bite one or more opossums and especially the agile, swift-footed cat in an area with numerous woodlots. Even if a rabid skunk should corner an opossum or cat in a burrow or deserted building, it is possible that the skunk would not survive the confrontation. In confined combat with either an adult opossum or cat, a rabid striped skunk could be killed. Therefore, rabid skunks might be able to bite a limited number of opossums and cats, but several considerations argue against the concept that the abundance of rabies seropositive opossums and cats resulted from bite transmission from clinically rabid skunks.

While it seems unlikely that clinically rabid skunks served as a source of rabies infection for opossums, it is conceivable that rabies infected opossums served as a source of the virus among skunks. One opossum which appeared normal at the time of capture had rabies antigen in its salivary gland. Opossums such as this one could serve to infect skunks, cats, or other opossums. Considering the demanding criteria necessary to distinguish between an animal progressing toward clinical rabies from a chronic rabies carrier, the study cannot state at the present time that opossums are the ultimate rabies reservoir in the sense that opossums disseminate the virus in their saliva while remaining asymptomatic carriers. However, from an evolutionary viewpoint regarding the maintenance and circulation of the rabies virus, it would seem disadvantageous for such widespread exposures, as suggested by the serum survey data among opossums, to represent complete "dead-ends" for the virus. A series of critical questions on this matter remains unresolved. Several of these questions are:

1. To what extend do opossums serve to maintain and transmit the rabies virus?

2. To what extent is rabies transmitted by opossums intraspecifically and/or interspecifically?

3. If opossums are refractory to clinical rabies with the aberrant behavior considered to be conducive for viral transmission by biting, as suggested by Barr (1961:63-64), what mechanisms of transmission exist among rabies infected opossums?

Answers to the important questions raised in the preceding paragraph must await future research, but some insights may be gained by examining the biological characteristics of the rabies seropositive opossums found in the study area. There was a strong indication that sex was not a factor which influenced rabies exposure among opossums. Overall the percentages of males, 15.7 percent (35/223), and females, 17.1 percent (66/385) with rabies antibodies were similar (Table 44, page 188). However, age as reflected by weight did appear to be a significant factor in the extent of rabies exposure. Based on the age categories established in this study, the extent of rabies exposure increased gradually as opossums progressed through their juvenile months, increased greatly as they aged from subadults to adults, and remained at a fairly constant percentage, approximately 20 percent, among adult opossums (Table 44, page 188). The gradual increase in the percentage of rabies seropositive opossums as the animals increase in weight suggests that the source of the virus was constantly present in the environment. However, the apparent persistence of the rabies virus does not imply a single source of the virus or a single mode of transmission.

Much of the serum survey data among opossums is consistent with some form of intraspecific circulation of the rabies virus among opossums. One possible mode of intraspecific transmission would be neonatal infection of the young by their mother. Reynolds (1953:92) noted that female opossums may lick their young as they crawl toward the pouch. If the saliva of the mother contained the rabies virus, infection of the young could occur. Young opossums normally make this move after a gestation period of only 13 days, and the ability of such poorly developed animals to respond immunologically to a rabies infection may be questionable. Barr (1961:31-32) found that young opossums at the age of 60 days were susceptible to rabies infection via intracerebral inoculation. Evidence of clinical disease was observed among two opossums, and another opossum developed an inapparent rabies infection which Barr considered to be an example of a carrier state. None of these opossum pouched young developed rabies infected saliva during the course of the study (Barr 1961:32), and none of 10 young opossums inoculated with rabies developed serum neutralizing antibodies (Barr 1961:

44, 83). These data suggest that neonatal rabies infections are possible among opossums, and some of these infections may remain subclinical during most or all of the life of the animal.

The study did find evidence of some rabies seropositive opossum pouched young (Table 42, page 183). At the present time the study cannot account for the occurrence of these rabies seropositive animals which were still in the pouch of their mother, both of which were rabies seronegative. It is possible that there was a transfer of specific or nonspecific immunological substances from the mother. Bell et al. (1970:1055) noted that they had previously demonstrated that rabies antibodies could be transferred in white mice from dam to offspring by suckling.

Some young opossums were apparently exposed to rabies during the first few months of independent life. The percentage of rabies seropositive opossums increased from 3 percent (1/35) for the smallest independent opossums to 7 percent (5/68) among opossums considered to be subadults (Table 44, page 188). However, the greatest increase in the percentage of rabies seropositive animals in the opossum population occurred as the young progressed from subadults to adults. This time would correspond, to some extent, with the winter months. As previously mentioned, these months may also be the time of year when skunks were exposed to rabies, and many of the same epizootiological factors may be responsible. Such factors as (1) intraspecific contact during the mating season, (2) inter- and intraspecific communal denning, and/or (3) contact with clinically rabid animals could produce a rise in the rabies seropositive portion of the opossum population. The concurrent use of a winter den by a striped skunk and an opossum have been recorded by Allen (1939:224) and Shirer and Fitch (1970:501). Such intimate association would facilitate the transmission of rabies.

The portion of rabies seropositive opossums did not increase among adult opossums. The opossums considered to be more than 10 months of age, weight classes 5-7, contained many opossums which had passed through their first winter of life and approximately one-fifth of these opossums were found to be rabies seropositive. This constancy in the portion of rabies seropositive opossums in the three heaviest weight classes may have reflected a species determined level on the number of individuals which produced detectable antibodies or the rapid removal of animals in this segment of the population.

The precise explanation for the fact that some opossums were rabies seropositive by the RFFIT, but were subsequently found rabies seronegative by the SN test is unclear. The animals found positive by both tests were designated as DRSP (Fig. 7, page 43) and may have represented animals which had been exposed to rabies more than once rather than animals which had received a single, large rabies infection. Regarding opossums, it is possible that young opossums are initially exposed to rabies as neonates or juveniles and develop low levels of rabies antibodies which are detectable only by the RFFIT, presumptive rabies seropositive opossums. In later life, perhaps during their first winter, a small portion of these PRSP opossums are exposed a second time. Such a second rabies exposure might produce a secondary immune response and a rabies antibody titer detectable by both the RFFIT and the SN test, a definitive rabies seropositive (DRSP) opossum. In discussing the secondary immune response among laboratory animals, Carpenter (1975:84) stated that:

> A second or subsequent injection of the same antigen at a considerable interval after the preceding injection usually causes a more rapid rise in titer than the first inoculation, the peak attained is greater, and antibody persists for a longer period. This is the secondary response.

If DRSP opossums were those animals which had received more than one exposure to the rabies virus, then it is not surprising that these individuals were exclusively adults.

If the more detectable antibody presence found among DRSP opossums was the result of a single, large infective dose of the rabies virus such as that which might be present in the saliva of a clinically rabid skunk (Sikes 1962:1044), then some subadult and juvenile opossums might be found among the DRSP animals. During the months between May and July nonadult opossums composed between 14 and 47 percent of the opossums captured (Table 24, page 107). If contact with a clinically rabid skunk was the source of the more detectable SN antibody response among opossums, then the nonadult segment of the population should be exposed in a percentage roughly equivalent to its abundance. However, there were no DRSP opossums among those animals considered to be nonadults (Table 37, page 163).

A major epizootiological implication suggested by the serum survey data was that the rabies virus persisted in the study area throughout the study. Considering only opossums the percentage found to be rabies seropositive was 15 percent (10/65) during 1973 (Table 32, page 147), 22 percent (43/192) during 1974 (Table 34, page 153), 15 percent (44/298) during 1975 (Table 37, page 163), and 8 percent (4/53) during 1976 (Table 41, page 178). These data would suggest that any periodicity among reported rabies cases was not dictated solely by a reintroduction of the rabies virus.

The factors influencing the geographical distribution of rabies seropositive animals were difficult to evaluate. In many instances the presence of rabies seropositive opossums and cats was related geographically to past, current, or future reported rabies cases. While the exact relationship between clinical rabies cases and rabies seropositive animals cannot be defined, the overlap in their distribution did appear to delineate areas of considerable rabies virus circulation. However, in other parts of the study area such as

Cocke County and southwestern Greene County rabies seropositive animals seemed to exist in the absence of any reported rabies cases. The fact that rabies seropositive animals were more widely distributed than the reported cases of clinical rabies does suggest that the rabies virus was circulated in areas beyond the focal areas where clinical rabies cases were concentrated.

The apparent association of rabies seropositive opossums with the major rivers of Cocke County (Fig. 37, page 199) cannot be explained at the present time. It may be postulated that a focal area of rabies infected animals existed in the northern part of the county where several large rivers come together, and that the presence of rabies infected animals radiated outward along these rivers. However, it is not possible to determine whether this pattern reflected an outward radiation of rabies infection, an inward flow of rabies infection toward the focal area, or a stable pattern based on different environmental factors. The pattern seen among rabies seropositive animals in Cocke County is further complicated by the fact that rabies seropositive animals in Jefferson and Greene counties were not strongly associated with major lakes and rivers. More research is certainly necessary on the ecological and epizootiological factors which influenced the presence of rabies seropositive opossums and cats. One factor, however, which did not appear to influence the presence or abundance of rabies seropositive opossums was the population density of opossums as expressed by the capture rate among the trap areas.

In summary, some of the major epizootiological implications of the serum survey data are:

1. Many opossums and cats were apparently exposed to the rabies virus without being involved in the reported cases of clinical rabies during the study.

2. Considering the apparent abundance of rabies seropositive opossums and cats in relation to the number of clinically rabid skunks which may have existed in the study area, bite transmission by clinically rabid skunks did not seem to be the most likely source of rabies exposure among cats and opossums.

3. The geographical distribution of reported rabies cases and rabies seropositive animals also argues against the bite of clinically rabid animals as a source of rabies exposure among cats and opossums.

4. The presence of rabies antigen in the salivary gland of one opossum, very young rabies seropositive opossums, and a gradual increase in the proportion of rabies seropositive opossums with age suggest the possibility of an intraspecific rabies cycle among this specific.

5. The consistent presence of rabies seropositive animals over the years of the survey suggests that the rabies virus was circulated continuously within the study area with no direct correlation with the periodicity of reported rabies cases.

6. Because of the widespread distribution and persistence of rabies seropositive animals within the study area, the results of the serum survey did not provide a clear, precise means for predicting the time and place at which clinical rabies cases might occur.

The data from the serum survey have one major control implication. The fact that the rabies virus was circulated in many parts of the study area outside the geographical foci of reported rabies cases means that any effort directed toward eliminating the virus within the focal areas might not be productive in the long term. It is possible that clinical rabies cases in the study area resulted from a temporal and spatial overlap of special environmental and/or host population attributes, and not strictly from the presence of the rabies virus. This concept would suggest that the primary objective of rabies control research should be to define the factors responsible for the concentration of clinical rabies cases in time, space, and species. Once these controlling factors are established, efforts can be directed toward reducing the incidence of the disease in wildlife populations.

VI. EPIZOOTIOLOGY OF RABIES IN THE STUDY AREA, 1972-1976

It is a basic tenet of science that before one can reach the correct answers to a complex problem, one must first ask the correct questions. Much of the present study was a search for patterns and trends which were valuable in their own right, but also presented clearly defined questions on the ecology of rabies. The study did, in fact, find many characteristic patterns and trends, some of which were based on strong data while others were only suggested. Considering the multitude of variables inherent in such a field study, the factors which created the patterns and trends found in this study may only be approached by speculation. Certainly, there is a great need for future research to clarify the factors responsible for many of the specific findings of the present study.

The epizootiology of sylvatic rabies is extremely complex and based upon a number of interrelated factors. Three of the most important factors are (1) the mean(s) whereby the rabies is maintained, i.e., the reservoir(s) of the disease agent, (2) the method(s) of viral transmission, and (3) the factor(s) which can initiate clinical disease following rabies infection. The information gathered during this investigation does not permit the rejection or establishment of any single concept regarding the overall epizootiology of rabies in wildlife populations. The disease agent may be circulated solely by clinically rabid animals, maintained as latent infections among the major host species and periodically reactivated, carried by inapparent reservoir species such as bats and periodically introduced directly into wildlife populations, or any of several other theories on sylvatic rabies ecology. This section will address these three major areas of rabies ecology, and this discussion will seek to stimulate future research rather than present concepts which the study believes to be firmly established.

Regarding the first major issue, the mode(s) of viral maintenance, the study cannot propose a definitive reservoir for the rabies virus in the study area. The virus did appear to persist in the study area during periods with few reported cases of clinical rabies. This persistence suggested that there was a reservoir of the virus in the study area. The study has attempted to differentiate between rabies infected animals, animals with rabies antibodies due to past rabies infections or current subclinical rabies infections, and clinically rabid animals, animals with severe central nervous system disease. Implicit in this distinction is the idea that the rabies virus may be maintained by one or more species of terrestrial wildlife species which were among those occasionally reported with clinical rabies and/or sampled during the serum survey.

While the true reservoir mechanism cannot be established, several points are suggested by the study data. The low abundance of skunks in relation to opossums and cats suggests that skunks were not a likely source of the rabies virus for the many opossums and cats found to be rabies seropositive. Since the domestic cat has a high susceptibility to rabies (Appendix A, Table 48) and may develop violent behavior when clinically rabid (Vaughn 1975:144-145), the fact that reported cases of cat rabies have been absent from the study area since 1965 (Appendix H) suggests that this species was not the primary reservoir of the rabies virus in the study area.

Theoretically, the opossum could serve as a reservoir of the rabies virus. Since the reservoir of an infection is the animate or inanimate material in which the infectious agent propagates and upon which it is most dependent for survival (Schwabe 1969:202), it may be expected that the disease agent-reservoir host would evolve toward a state of mutual tolerance in which the host animals would not be subject to clinical disease (Fenje 1968:219). The opossum appears to have a natural resistance to clinical disease produced by the rabies virus (Barr 1961:46), and yet, as the study demonstrated, some opossums may develop the ability to shed the virus. However, the study was unable to determine whether opossums served as a source of rabies virus for striped skunks, free-roaming domestic cats, or other opossums. If opossums did serve as a vector of the rabies virus, there is no explanation for the predominance of skunks among reported rabies cases. Chronic rabies carriers among opossums, if they existed, might be expected to have contact with unvaccinated house pets, raccoons, foxes, and other wild mammals on a level proportional to their abundance. If opossums were the major reservoir of the rabies virus, it is likely that a greater diversity of species might be infected and develop clinical rabies.

This study would suggest that the reservoir of the rabies virus was not in any single species, but consisted of members of several wildlife species which maintain the virus through subclinical rabies infections. Regarding raccoon rabies in Florida, Bigler et al. (1973:333) suggested that "many raccoons develop subclinical infections." Verts (1967:174) suggested that young striped skunks might acquire a latent rabies infection from their mother. McLean (1970:232) stated that:

> The host species that maintain the enzootic foci by intraspecific reservoir mechanisms are most likely the same as the major hosts of wildlife rabies reported from those areas, and the hosts that support epizootic.

Other evidence has accumulated during recent years which indicate that rabies infections do not invariably lead to death (Doege and Northrop 1974, Bell 1975). While the exact physiological mechanism whereby the virus may be maintained in the body during long asymptomatic periods is debatable, the overall concept may be similar to the epidemiology of the poliovirus or to that of such slow viral diseases as scrapie and transmissible mink encephalopathy.

The rabies virus and the poliovirus are taxonomically different, but they both produce clinical disease only after infecting the central nervous system. In discussing the poliovirus Fenner and White (1976:335-338) stated:

> It is important to realize that paralysis is a relatively infrequent complication of an otherwise trivial infection. Of those infections that become clinically manifest at all, most take the form of a minor illness . . . . It is only in the occasional case that the central nervous system becomes involved. . . . The probability of neural involvement with consequent paralysis is influenced by certain well-defined factors, notably age, pregnancy, tonsillectomy, trauma, fatigue, and inoculation. . . . The chain of infection is rarely obvious, because most infections are inapparent.

An analogy between the rabies virus and the poliovirus was suggested by Johnson (1960:268) who stated:

> The capacity of rabies virus to multiply in a variety of organs such as salivary glands, kidneys, and breast tissue makes it possible for the virus to have cycles of infection not associated with encephalitis. . . . There is considerable similarity between the rabies virus and the poliomyelitis viruses of man and certain animals, and we must consider the possibility that rabies virus may, under certain circumstances, survive as an intestinal tract infection.

Therefore, the poliovirus may serve as one model of a disease agent which under most environmental situations does not cause clinical disease and continues to be transmitted while retaining the capacity, under certain environmental conditions, to create severe disease. Theoretically, the rabies virus could possess similar attributes, and be maintained within the visible rabies host species as well as other wildlife populations.

The concept that rabies may be a slow viral infection akin to scrapie in sheep or kuru in man has been recently suggested. Debbie (1974:241) stated:

> The occasionally very long and often erratic incubation period of the disease prior to the emergence of overt signs has been the primary basis for considering rabies as a "slow virus" infection.

Gajdusek (1977:974) also included rabies among "slow infections of animals caused by conventional viruses." While much remains to be clarified regarding this concept of rabies, the central feature of this hypothesis would appear to be that an inherent characteristic of naturally acquired rabies infections under nonepizootic conditions is a prolonged subclinical stage during which the virus progresses toward the clinical stage over many months or even years. Such long periods of asymptomatic maintenance in relatively short-lived wild animals, if they occur, could constitute a reservoir mechanism for the rabies virus. The characterization of the rabies virus as a slow viral infection would not necessarily be applicable to the epizootic situation, but the slow progression toward clinical disease may represent one end of a continuum with the rapid spread by the biting of clinically rabid animals at the opposite extreme. Therefore, the study would agree with the suggestion of McLean (1970:232) that "in the enzootic state, a slow, continuous circulation of the virus within the maintaining host population must occur by subclinical, mild and chronic, or lethal but prolonged infections."

The second major epizootiological issue, the method(s) of viral transmission, is also a critical factor in rabies ecology. Certainly, rabies transmission by the bite of a clinically rabid animal or an animal progressing toward clinical rabies is a well established mode of viral transmission. While bite transmission by clinically rabid animals is the most dramatic and visible form of rabies transmission from a human perspective, these considerations alone do not dictate the exclusive transfer of the virus by this means.

As previously noted, some wild animals infected with rabies may only develop subclinical infections and never develop the central nervous system disorders of clinical rabies. Furthermore, some animals with rabies infections or clinical rabies may not produce rabies infected saliva (Sikes 1962:1045, Parker and Wilsnack 1966:36, Verts 1967:167). Some rabies infected animals may not exhibit the aggressive behavior conducive to the spread of rabies by vicious biting attacks (Bigler et al. 1973:333, Gough and Niemeyer 1975: 173). If some, perhaps a majority, of rabies infections produce only subclinical infections, then the aberrant behavior and vicious biting attacks associated with rabies transmission via infected saliva may play only a minor role in sylvatic rabies circulation over the long term. Furthermore, if rabies infected saliva in conjunction with aggressive behavior are not the predominant outcome of naturally acquired rabies infections, then bite transmission of rabies by clinically rabid animals would appear to be a rather haphazard mode of viral circulation. Wildlife rabies epizootics may represent relatively short abnormalities in the continual, nonvisible presence of rabies infected animals within a region. The mode of rabies transmission during an epizootic may not be the same as the mode of rabies transmission during the interepizootic period.

Some of the findings of the present study suggest that other forms of rabies transmission may have existed in the study area in addition to the classical bite mode. These findings include:

1. An annual peak or initiation of clinical rabies cases during the late winter-early spring which was usually separated from other peaks by several months with few, if any, reported rabies cases.

2. The abundance of rabies seropositive animals among species not associated with reported cases of clinical rabies in any year of the study.

3. The presence of rabies seropositive animals in areas of past or future reported rabies cases but free of any recent reported cases of clinically rabid animals.

Based on these data the study cannot offer a single mode of rabies transmission as an alternative to biting by clinically rabid animals. Theoretically, however, the major alternatives may include such intraspecific methods as (1) transplacental infection among placental mammals, (2) neonatal infection via infected milk or maternal contact, and (3) venereal transfer. The alternative methods possible for both intra- and interspecific transmission include (1) aerosol, (2) urinary, (3) casual biting not associated with aggressive behavior, and (4) ingestion of rabies infected tissue, primarily by carrion feeding. It is conceivable that several of these seven modes of rabies transmission may occur concurrently within areas such as northeastern Tennessee.

An analysis of rabies transmission in the study area can be based upon (1) the occurrence of reported cases of clinical rabies cases among skunks and (2) the serum survey data among opossums. In some ways these two sources seem to present conflicting ideas on rabies transmission. The former category would suggest that rabies is transferred primarily to adult skunks during late winter-early spring. However, the data from the serum survey suggest that some neonatal transmission occurred and that young opossums were exposed at a fairly uniform rate during their first year of life. It is possible that opossums served as a rabies source for skunks by some of the four methods of interspecific rabies transmission mentioned above. However, the first three forms of transmission might conceivably produce new rabies infections during the entire year and also create clinical rabies infections in a wide variety of species. On the other hand, carrion feeding as a source of rabies might be limited in time to the late winter months when wildlife mortality might be high, some food sources would be scarce, and feeding behavior by such potential scavengers as the skunk would be expanded to include any available food item. A detailed discussion of carrion feeding as a possible means of rabies transmission is presented in Appendix Q.

It is possible that a closed intraspecific cycle of rabies transmission existed among skunks in the study area. However, the low abundance of skunks suggested by the trap data does not favor the idea that intraspecific contact among adult skunks was common. While such contact may have been uncommon, one or more of the seven possible modes of intraspecific rabies transmission mentioned above could account for the presence of clinically rabid skunks in the study area, and the late winter peak in clinical cases could have resulted from the reactivation of infections acquired by young skunks or new infections acquired by breeding contact or communal denning.

Rabies exposure among opossums appeared to be quite widespread, and it is possible that some form of intraspecific methods, with the exception of transplacental infection, functioned in rabies circulation. The apparent presence of rabies seropositive pouched young and very young independent opossums suggests some form of neonatal transmission. The increase in the percentage of rabies seropositive opossums as they aged from subadults to adults suggests that additional rabies transmission occurred during the first winter in the lives of many opossums. This rabies infection may have occurred by venereal, aerosol, urinary, casual biting, or carrion feeding transmission. Venereal transmission may have been of limited significance because there was a steady increase in the percentage of rabies seropositive opossums over several juvenile and subadult weight classes (Table 44, page 188) which indicated that many young opossums were exposed to rabies prior to their first breeding season. Rabies transmission by aerosol and urine may not have been of major importance. The rabies virus may not remain infective for long periods outside the body. Bruner and Gillespie (1973:1152) stated that the rabies virus in thin layers is readily inactivated by ultraviolet light and that the virus in dried saliva loses virulence within a few hours at ordinary temperatures. Therefore, sunlight could destroy the infectivity of the rabies virus. A major role for casual biting in situations not associated with the breeding season may also be doubtful. Lay (1942:149) stated that "opossums generally den and feed alone, but are tolerant to neighbors."

Carrion feeding is a viable possibility for rabies transmission among opossums. The experimental evidence for oral transmission of rabies is given in Appendix Q. This form of rabies circulation among opossums may result from several characteristics of opossum ecology. First, opossums may live at high densities (Holmes and Sanderson 1965:290, Lay 1942:151, Fitch and Sandidge 1953:334-335) and the home ranges of opossums may overlap to a large extent (Fitch and Shirer 1970:174). Secondly, opossums are omnivores which may feed on carrion (Reynolds 1945:369, Lowery 1974: 60). Thirdly, opossums may develop subclinical rabies infections (Barr 1961:32). Based on these considerations it is possible to hypothesize that after a rabies infected opossum dies, the carcass could be consumed by other opossums and an invisible chain of rabies infection established.

The preceding discussion regarding rabies transmission is largely speculative. The accumulated data of the present study suggest that some mode(s) of rabies transmission other than the classic bite route did exist among the wild and feral animals in the study area. The precise nature of such alternative transmission route(s) could not be determined, but this important element of sylvatic rabies ecology certainly deserves further investigation.

The third and final issue of rabies ecology involves the factors which may serve to initiate clinical rabies following the establishment of a rabies infection. This section of the discussion has suggested that rabies may be maintained asymptomatically by members of several wildlife species and transmitted by means other than the vicious biting attacks associated with the clinical disease. Taken together, these theories may be extrapolated to suggest that clinical rabies is not an integral part of rabies ecology. If the ecology of rabies was dictated by an unbroken chain of random biting attacks by clinically rabid animals, then distinct patterns of reported rabies cases in species, time, and space might not exist. However, the data on reported rabies cases in the study area suggest that clinical rabies, as an overt disease entity, was clustered in species, time, and space. Such clustering may indicate that certain factors served to initiate clinical rabies from only a segment of the animals infected continuously over a wide area.

Perhaps the most intriguing aspect of clinical rabies was the predominance of recognized cases in only one species, the striped skunk. The serum survey data suggested that both cats and opossums were exposed to the rabies virus, but such exposures apparently did not result in many clinical rabies cases. Such a situation could result from either (1) a special pathogenic "strain" of the rabies virus circulated intraspecially among skunks while a less pathogenic type of rabies was present among opossums and cats or (2) a single type of the rabies virus with a special virus-host relationship with skunks which was mediated by mutual evolution and conducive to producing clinical rabies cases under certain environmental circumstances. The present study did not investigate the antigenic nature of the rabies virus in the study area, but the factors responsible for the apparent concentration of clinical rabies in a single species after other shifts in the major rabies host species are certainly critical in understanding the ecology of rabies and they merit more comprehensive investigations in the future.

The factor of time in the ecology of rabies was also interesting. The occurrence of reported skunk rabies cases within the study area in time seemed dependent on three factors. These factors were (1) a period of years sufficient for rabies infection among skunks to move into the area from that part of the study region where the earliest skunk rabies cases were reported, (2) a multi-year cycle with peaks of reported cases separated by from two to four years, and (3) an annual cycle with peaks of reported skunk rabies cases in late winter-early spring. The various factors which may have influenced these temporal patterns and trends have been discussed previously, but they seem to suggest that some attribute(s) of the host population influenced the temporal pattern of clinical rabies cases. The concept that the temporal pattern of clinical rabies cases within a given species may have been influenced by characteristics intrinsic to that species is reinforced by data which suggest that the epizootiological pattern of clinical rabies changed, to some extent, as the major rabies host species shifted. The concept that different host species have different patterns of clinical rabies incidence would suggest that some host factors, perhaps in conjunction with rabies virus modification, strongly influenced the occurrence of clinical rabies cases in time.

The spatial pattern among reported rabies cases appeared to be dependent on two factors. These factors were (1) macrofoci which developed within the valley portion of the study region following the radiation of rabies infection among skunks and (2) microfoci which developed within the study area. Within the study area it was noted that the microfoci were not the exclusive range of either the rabies virus or the major host species, the striped skunk. Therefore, it may be postulated that some environmental attribute of these microfoci, either through a positive or negative influence on striped skunks, dictated the occurrence of clinical rabies cases in space. A highly speculative theory would be that the microfoci were areas where skunks had extended life spans which were sufficient to allow rabies, as a slow virus infection, to reach the clinical stage. Another suggestion would be that the microfoci were areas of suboptimal skunk habitat where a variety of stresses reduced disease resistance and/or altered behavior. Areas of suboptimal habitat might produce more communal denning, more animal contact due to longer forays for food, more malnutrition, and more reliance on carrion feeding. However, the precise environmental determinants which produced both the macro- and microfoci could not be determined, and the entire landscape epizootiology of rabies in northeastern Tennessee should be examined in greater detail by future investigations.

In summary, the present study would suggest that the occurrence of clinical rabies was dictated by factors other than the mere transfer of the rabies virus. The study would tentatively propose that clinical rabies is an anomaly which occurs infrequently among many subclinical rabies infections. Furthermore, the study would postulate that most rabies infections are not acquired through a vicious biting attack associated with clinical rabies except during large rabies epizootics which are themselves anomalous situations. The presence of a special virus-host relationship may have resulted in the predominance of skunks among clinical rabies cases. The restriction of clinical rabies cases in time and space may have resulted from a number of factors such as environmental stresses localized in time and space and/or the character of host population immunity. However,much work remains before these critical aspects of rabies ecology can be truly elucidated.

Much of the data gathered in this study may raise more questions than they answer, but these findings may serve to cast doubt on old theories, indicate new directions for future work, and stimulate researchers to seek new answers concerning the enigma which Charles Darwin referred to as "so strange and dreadful a disease" (Darwin 1839). If this study should only serve to generate new ideas on this old problem, it will have fulfilled its ultimate objective.

THE ECOLOGY OF RABIES IN
NORTHEASTERN TENNESSEE

A Dissertation
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Doctor of Philosophy
Degree
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VOLUME II

CHAPTER IV

CONCLUSIONS

The major conclusions of the study were directed in response to the six study objectives. The conclusions were:

1. The study concluded that clinical rabies within the study region was a dynamic disease entity. The most pronounced changes in the epizootiology of clinical rabies involved the major host species among reported cases. The major host species of clinical rabies changed from the dog, to the fox, and most recently to the skunk. These shifts in the major rabies host appeared to involve a gradual reduction in the number of counties experiencing reported rabies cases, and there were some alterations in the sections of the study region with reported rabies cases. The shift from the period of fox rabies to skunk rabies appeared to result in a change from yearly cases of rabid animals to a periodicity of rabies cases separated by two to four years. The exact means whereby rabies was introduced into the skunk population remain unclear, but the initial reports of rabid skunks occurred in areas with a very persistent fox rabies problem. After the initial occurrence of clinically rabid skunks in the study region, cases of rabid skunks appeared to radiate southward into northeastern Tennessee. At the present time the precise reasons for these major changes in the epizootiology

of rabies cannot be determined, but the study did conclude that such pronounced changes were not dictated solely by biases in the rabies reporting system.

2. The study concluded that recent reported rabies cases within the study area were not randomly distributed in space. On a large scale Cocke County was entirely free of reported rabies cases, perhaps as a result of the large river systems which may have interrupted the southward movement of rabies infection among skunks. Within the other two counties the earliest or only reported rabies cases of each year occurred within relatively localized areas which were considered to be microfoci of clinical rabies. These microfoci were not unique in the presence of rabies seropositive animals, striped skunks inhabitation, the presence of human population centers, recognized caves, or major topographical features. Statistically, these microfoci of clinically rabid skunks were (1) farther away from major lakes and rivers and (2) freer of forest/woodland cover than areas with striped skunks not associated with reported skunk rabies cases. While the degree to which these microfoci were preferred or suboptimal striped skunk habitat could not be determined, these areas may have contained environmental features conducive to the acquisition or reactivation of rabies infections. The failure to capture striped skunks in 45 of the 48 trap areas suggests that the microfoci were not unique in striped skunk population density.

3. The study concluded that recent reported rabies cases within the study area were not randomly distributed among the months of the year. The annual peak of reported rabies cases occurred during the March-April period, and during four of the five years between 1972 and 1976 the initial reported rabies case of the year occurred during this two-month period. These data suggest that the rabies virus was not transmitted throughout the year by means of bite transmission from clinically rabid animals. Within the study area some form of biological reservoir mechanism such as subclinical rabies infections may have maintained the virus during the late summer to mid-winter period. It remains unclear as to whether the late winter upsurge in reported rabies cases resulted from newly acquired infections proceeding directly into the clinical disease or the reactivation of latent, long-term rabies infections. The apparent peak in clinical rabies cases among skunks coincides roughly with the time of (1) striped skunk breeding activities, (2) the most likely time for intra- and interspecific communal denning, and (3) a possible time of poor food supplies and diminished fat reserves which might increase mortality, alter feeding habits, and increase the reliance of skunks on scavenging. The extent to which any one or all of the above factors contributed to the annual peak of clinically rabid skunks could not be determined.

4. The study was unable to determine the role of sex

upon the incidence of clinical rabies among striped skunks, but the majority of reported skunk rabies cases apparently occurred among adults. The general absence of clinical skunk rabies cases in the fall of the year may have reflected a small juvenile skunk population, and indirectly indicated a small breeding population of skunks in the study area. A basic conclusion of the study was that striped skunks were not abundant in the study area in spite of the fact that 47 skunk rabies cases were reported during the 1972-1976 period.

The limited data on skunk population dynamics suggested several tentative conclusions regarding the interrelationship between skunk abundance (as indicated by the collection of skunk pelts by commercial trappers) and the incidence of reported skunk rabies cases. These conclusions were:

(1) The transition of the skunk from an incidental rabies host to the major rabies host species followed several years of decline in skunk abundance.

(2) The periodic upsurges in reported skunk rabies cases did not appear to be density dependent phenomena in the sense that they occurred during periods of abnormally high skunk population densities.

These two tentative conclusions suggest that the initial occurrence of clinically rabid skunks may have occurred in populations experiencing decline due to some type of environmental stress, and that the periodicity of the minor skunk rabies outbreaks may have been related to alterations in the population immune status or periodic influxes of skunks from other areas.

5. The study concluded that some opossums and free-roaming domestic cats captured in the study area were rabies seropositive, and one of the three striped skunks tested was rabies seropositive. Among the seven rabies seropositive opossums tested, one had rabies antigen in a sample of its salivary gland. Because serum sampling was more extensive among opossums, data regarding this species formed the basis for analyzing the serum survey. The study concluded that some opossums may be exposed to rabies as neonates, but that additional exposures occurred during both the juvenile and subadult age classes. By the time opossums reach adulthood, it is conceivable that practically the entire age category may have been exposed to the rabies virus with approximately 15 to 20 percent of the animals forming detectable antibodies. The sex of opossums did not appear to influence the degree of rabies exposure. The study concluded that clinically rabid skunks were not the most likely source of rabies exposure among opossums, and that some form of intraspecific rabies transmission among opossums was a possibility. The degree to which rabies infected opossums may have served as an interspecific disseminator of rabies could not be determined.

Based on the serum survey data the study concluded that the rabies virus was maintained in the study area throughout the years of the study, and that the virus was circulated in areas other than the microfoci of reported rabies cases. Certain parts of the study area had relatively high levels of rabies seropositive opossums without any reported rabies cases, and these areas were situated in parts of the study area where an abundance of clinically rabid animals might be expected to produce some reported cases. Because rabies seropositive animals were widely distributed and present during each year of sampling, the study concluded that the serum survey data were not sufficient for the precise prediction of the time and place of clinically rabid animals.

6. The data accumulated during this study did not permit the establishment or rejection of any single concept regarding the epizootiology of rabies in wildlife populations, but the data did allow for limited speculations concerning the three major elements of rabies ecology. First, the study postulates that the rabies virus may have been maintained by means of subclinical infections in many members of the major host species, the striped skunk, and other species not associated with recognized cases of clinical rabies. Secondly, the study postulates that if clinical rabies is an infrequent outcome of rabies infection, then rabies transmission must occur primarily in a manner not related to the vicious biting attacks associated with clinical rabies. At the present time a precise alternative mode of rabies

transmission among terrestrial wildlife with asymptomatic rabies infections cannot be established, but such means as neonatal infection, urinary, aerosol, venereal, casual biting, and oral infection via carrion feeding may be involved. Thirdly, the factors which may initiate clinical rabies from a subclinical rabies infection remain unclear, but the apparent concentration of clinical rabies cases in time, space, and species suggests that clinical rabies may be a function of factors other than the mere transfer of the virus. The occurrence of clinical rabies may be related to such factors as the "strain" of the rabies virus, immune status of host population, suitability of the environment, and/or the physiology of host animals. Such factors may play a critical role in producing disease from what otherwise may be only a trivial infection.

Perhaps, the single most important conclusion of the present study is that much more work remains to be done before the basic facts regarding the epizootiology of rabies can be established. This work should be undertaken for more than academic reasons, because the full elucidation of rabies epizootiology must precede any truly effective control of the disease. Furthermore, clinical rabies in wildlife populations may be a reflection of serious perturbations in the ecosystem. Therefore, the occurrence of clinically rabid wild animals may signal more than the necessity to control a viral disease, but may also indicate the need to create a more inhabitable environment for our valuable wildlife resources.

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APPENDICES

APPENDIX A

RABIES, CLINICAL ASPECTS

APPENDIX A

RABIES, CLINICAL ASPECTS

Rabies as a clinical disease may be defined as "an acute infectious disease of the central nervous system caused by a virus" (Sikes 1970:3). The causative agent, the rabies virus, is composed of a single strand of RNA, and it has been classified with the rabies group of the rhabdoviruses (WHO 1973:6, 14). The basic morphology, chemical composition, structural antigens, dynamics of replication, and virus/host cell interaction of the rabies virus are known (Wiktor 1971: 38-49, Murphy 1975:33-61).

The source of rabies infection is generally considered to be the bite of an infected animal with rabies virus in the saliva. Transmission by such biting is thought to have the greatest epizootiological significance (Verts 1967:145). Under certain circumstances aerosol transmission is possible (Constantine 1967a:30). While aerosol transmission is usually associated with the infection of man and animals by bats, Winkler et al. (1972a:276) indicated that under special conditions airborne transmission between carnivores might be possible. Transmission may also occur by the ingestion of rabies infected tissue (Soave 1966:45, Bell and Moore 1971: 179, Ramsden and Johnston 1975:323). The possibility of transmission via rabies infected urine was indicated by

Fischman and Schaeffer (1971:90,94) and Debbie and Trimarchi (1970:503-504). There is evidence to indicate that no arthropod vectors are involved in the transmission of rabies (Bell et al. 1957:279, Constantine 1967a:18).

Regardless of the mode of transmission, once infection has occurred, at least four courses of events are possible. These courses are: (1) abortive infection, (2) a chronic carrier state, (3) a latent infection, and (4) the development of the clinical disease following an incubation period. The factor or factors that determine which course follows the initial infection are unclear.

Abortive rabies refers to the termination of the pathological effects of the virus on the host without implying whether the virus ceases to infect the host. Abortive rabies infections have been reported among dogs (Bell 1966a:171), and nonfatal rabies infections may occur in some terrestrial wildlife (Bell 1966b:19). Nonsusceptibility resulting from the genetic characteristics of a species would probably result in abortive infections.

In the chronic carrier state an animal would not develop the clinical disease, but would remain healthy and shed infective virus. Chronic carriers would be capable of infecting other animals over an extended time period. In large bat colonies apparently healthy bats may spread infective rabies virus in aerosol form or by casual biting (Constantine 1971:256). However, several studies have been unable to demonstrate conclusively that the chronic carrier state exists in North American bats (Bell 1966b:18, Johnson 1971:247). While striped skunks have been shown to excrete the virus in their saliva for several days prior to the onset of any rabies symptoms (Sikes 1962:1044), there is no evidence to indicate that either the fox or skunk in North America can become chronic rabies carriers.

The third possible outcome of rabies infection is latent rabies. A latent infection refers to a condition in which the disease agent persists in the tissues for long periods during which there are no obvious manifestations of disease. This term is not used in situations where the incubation period may be quite long. In contrast to chronic carriers, animals with latent rabies infections may not be capable of infecting other animals. One important aspect of latent infections is that there must be a reactivation of the disease agent before the clinical disease and/or shedding of the agent can occur. In the latent state the disease agent is hidden and may be at a dead end unless the host's internal or external environment triggers reactivation.

Definitive proof of latent rabies infections in the foxes and Mustelidae of Central Europe and the United States has not been found (WHO 1973:39). However, several studies have speculated that latent rabies infections in terrestrial wildlife are possible. Verts (1967:174-176) stated that young striped skunks may receive an <u>in utero</u> latent rabies infection. McLean (1975:75) suggested that latent, sublethal rabies infections may be one of the biological reservoir mechanisms which allow the virus to be maintained in raccoon populations between epizootics.

The development of clinical rabies is the remaining course of events following infection. After infection rabies symptoms may occur within a few days or after several months. The clinical disease is preceded by a period of incubation. Recorded durations for the incubation period among wildlife species are quite varied (Table 47), and the factors responsible for this variability both within and among species remain a significant problem in the epizootiology of rabies. The fact that skunks as well as other rabies hosts can have long incubation periods represents at least one possible mechanism for perpetuating rabies within a population over extended periods of time in the absence of overt rabies cases.

The length of the incubation period has been associated with several factors including the physical condition of the animal, stress, site of inoculation, and the "strain" of the rabies virus in the infecting dose (Winkler 1975:14). The duration of the incubation period seems to be inversely related to the amount of rabies virus in the infecting dose (Sikes 1962:1043). Baer and Cleary (1972:523-524) presented evidence to indicate that the virus remains at the site of introduction for most of the incubation period. Murphy et al. (1973a:374) stated that "intramuscular harborage" prior to

Table 47. Recorded incubation periods for rabies among several terrestrial wildlife species.

Species	Duration of incubation period (in days)	Source
Gray fox and red fox	12-109	Sikes 1962: 1042-1043
Red fox	14-57	Parker and Wilsnack 1966: 35
Striped skunk	14-172	Parker and Wilsnack 1966: 35
	14-88	Sikes 1962: 1042-1043
	20-71	Niemeyer 1973:38
Opossum	14-44[a]	Constantine 1967a:51
	30	Sikes and Tierkel 1962: 270
Raccoon	10-42	Sikes and Tierkel 1962: 270
	79+	Bigler et al. 1973:333

[a]Incubation period given here is the interval from the day the animal entered the cave until it showed symptoms.

the infection of nerve cells may account for long and/or variable incubation periods.

After the rabies virus infects peripheral nerve tissue, there is a centripetal movement of infection toward the central nervous system (CNS) (Sikes 1970:11). Within the CNS rabies virus causes inflammation and some degeneration of nerve cells. From the CNS there is a centrifugal spread of the virus to other parts of the body (Schneider 1975:289). This spreading may result in the extraneural infection of the pancreas, adipose tissue, and myocardium (Murphy et al. 1973b:1). Johnson (1966:29) noted that the rabies virus has an attraction for the lungs, mammary glands, kidneys, and muscle tissue. The proliferation of the virus in the lungs and/or oronasal cavity of the host would facilitate airborne transmission.

The duration of the clinical illness is an important factor in the transmission of rabies. The dumb or paralytic type of the disease does not favor classical bite transmission because the paralysis of the jaws hinders the ability to bite, and the overall duration of this form is shorter than furious rabies (Kaplan 1969:423). Sikes (1970:11) stated that laboratory studies on wildlife show that a majority of animals develop the furious form of rabies, but Gough and Niemeyer (1975:173) found that in a laboratory epizootic, most of the striped skunks which died of rabies showed no clinical signs of illness and rarely demonstrated aggressive behavior.

The duration of the overt disease is not equivalent to the period during which rabies virus is excreted in the saliva. Sikes (1962:1044) reported that experimentally infected striped skunks may have virus in their saliva from five days before to four days after clinical symptoms become apparent.

While rabies has long been considered a disease which invariably resulted in death (Tierkel 1959:192, Marx and Swink 1963:172), the idea that rabies is consistently fatal even after the development of overt symptoms has been challenged (Bell 1975:349-350). Evidence has been presented which indicates that recovery from rabies is possible in man (Bhatt et al. 1974:862) and in dogs (Arko et al. 1973:937).

The introduction of the rabies virus into a mammalian host can trigger an immune response by the body. One element of this response is the production of macromolecules known as serum neutralizing (SN) antibodies. In the laboratory the creation of SN antibodies to combat rabies infection has been induced by the inoculation of rabies virus into skunks and foxes (Sikes 1962:1046), opossums (Barr 1963:66), and dogs (Arko et al. 1973:937). These antibodies are created specifically to neutralize the rabies virus, and they are produced only in the presence of antigens unique to the rabies virus.

The exact role of rabies SN antibodies in the defense of the host against clinical rabies is not known (Bell 1975: 341-344). The presence of antibodies for a particular disease agent does not necessarily mean that the host is immune to that disease. It has been demonstrated that laboratory animals can survive rabies inoculation and not develop rabies SN antibodies (Parker and Sikes 1966:943, Barr 1963: 66). It has also been shown that some laboratory animals which die of rabies following an inoculation of rabies virus have significant levels, or titers, of rabies SN antibodies (Sikes 1962:1045, Parker and Sikes 1966:943). Serum neutralizing antibodies may be related to the development of latent rabies infections. Baer and Cleary (1972:525) suggested that a temporary antigen-antibody bond may form which does not destroy the antigen, but at a later time the bond may break and release the antigen.

While an animal may not produce SN antibodies in response to a rabies infection, the presence of such specific rabies antibodies is generally considered to be reliable evidence of past exposure to the rabies virus (Verts 1967: 148). Rabies antibodies do not necessarily constitute evidence of recovery from clinical rabies. Therefore, the detection of rabies SN antibodies in the serum of wild animals captured in the field can be interpreted to mean that the animals currently have, or previously had, a rabies virus infection (Tierkel 1959:189, Verts 1967:148, Mahon 1973:82, Everard et al. 1974:194).

APPENDIX B

RABIES, ECOLOGICAL ASPECTS

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RABIES, ECOLOGICAL ASPECTS

While clinical rabies among many groups of animals has been observed since ancient times, there is no evidence to indicate that rabies occurred in the New World prior to settlement by Europeans. However, it is possible that the disease was present in New World canines with a circumpolar distribution such as the wolf (*Canis lupus*). A thorough history of rabies and rabies research is given by Steele (1975).

Johnson (1959:406) stated that the first recorded rabies cases in the United States occurred among dogs. There were reports of rabid dogs in Virginia during 1753 and in North Carolina in 1762. He also noted that one of the first rabies outbreaks in wildlife occurred among foxes in Massachusetts during 1812. The first reference to skunk rabies came from reports of rabid spotted skunks in Lower California during 1826 (Johnson 1965:830). The group of native American animals in which rabies has been discovered most recently is the insectivorous bats with the first confirmed case occurring in Florida during 1953 (Venter et al. 1954). Data concerning rabies among nonhematophagous bats are summarized by Baer (1975).

Starting about the middle of this century, there has been a significant shift in the species composition of reported rabies cases. In the first half of the twentieth century the domestic dog was the most common host of rabies in the United States and Canada (Sikes 1970:4). An upsurge in the number of reported wildlife rabies cases began about 1940, and this trend continued through a transition period between 1951 and 1970 during which wildlife species became the most commonly infected group of animals (Winkler 1972a: 674).

Within this general shift from domestic animal rabies to wildlife rabies, several other trends are discernible. During the early 1950's fox rabies cases were more numerous than rabies cases among skunks (Scholtens and Tierkel 1963: 54). During the late 1950's skunk rabies cases increased while the number of rabid foxes decreased. Since 1961 rabid skunks have constituted the majority of the reported rabies cases in the United States. The number of reported bat rabies cases began to rise in the late 1950's, and the incidence of rabid raccoons has also increased in recent years.

The rabies virus has the capacity to infect all warm-blooded animals (Sikes 1970:3). Throughout the world clinical rabies has been recorded in a wide variety of species (Irvin 1970). Natural infections occur almost exclusively in mammals, and primarily in the mammalian orders of Chiroptera and Carnivora. Among the families of Carnivora, rabies appears predominantly in the Mustelidae, Viverridae, and Canidae.

Different species appear to vary widely in their susceptibility to rabies infection. In laboratory studies among several wildlife species, Sikes and Tierkel (1962: 269-270) showed that foxes had the least resistance to infection, and skunks, raccoons, and opossums had progressively more resistance. Much of the available data on the varying susceptibility among animals to rabies are summarized in Table 48.

One of the most critical aspects of rabies ecology is the reliability of data on the number of rabies cases reported from a given area. The records on animals submitted to a diagnostic laboratory and found to be rabid are generally the only information available on the prevalence of rabies in an area. Verts and Storm (1966:419) stated that these data do not accurately reflect the true level of rabies within the reporting area. Verts (1967:159) noted that local health officials may show different degrees of zeal for submitting animals for rabies diagnosis, and thus influence the level of reported cases. Smart (1970:81) stated that some authorities believe that "rabies reporting in rural areas is unreliable and provides a weak basis for detailed analysis." Jennings et al. (1960:177) reported that during an epizootic of fox rabies in Florida many foxes were killed while attacking men or domestic animals without actually biting, and these foxes were never reported. Parker (1962:279) observed that in some cases skunks which acted rabid were

Table 48. Variation in the susceptibility of various animal categories to rabies infection (based upon the intramuscularly inoculated dose required to infect at least 50 percent of the animals, unless otherwise indicated).

Susceptibility			
Extremely high	High	Moderate	Low
Fox	Skunk	Dog	Opossum
Coyote	Raccoon	Sheep[a]	
Wolf[a]	Domestic cat	Goat[a]	
Jackal[a]	Bat	Horse[a]	
Cotton rat	Bobcat	Nonhuman primate	
Field vole	Mongoose[a]		
Kangaroo rat	Other Viverridae[a]		
	Rabbit		
	Cow		
	Guinea pig		
	Hamster		
	Other rodents		

[a]Based on epideminological evidence only.

Source: WHO, 1973, WHO expert committee on rabies, sixth report, WHO Technical Report Series No. 523, World Health Organization, Geneva, 55 pp.

shot and considered as rabid with a laboratory diagnosis.

Many factors may bias the level of reported rabies. The most common consideration is that high human population densities and an increased awareness among the human population may result in a disproportionally high level of reported rabies (Rakowski and Andrews 1972:66-67, Smart 1970:52). However, in Illinois the number of rabid foxes did not parallel human population density, but did parallel county size, number of fox heads submitted, and the number of rabid skunks reported (Schnurrenberger et al. 1970a:1333). Lewis (1972:247) also noted that human population figures did not have a strong influence on the reporting rate of skunk rabies in Oklahoma. Marx (1966:119) suggested that the type of agriculture practiced in a particular area could affect the level of reported rabies. Lewis (1972:248) found that the level of skunk rabies in Oklahoma could be statistically related to several land use and environmental factors.

Regardless of the fallacies in rabies reporting, the information contained in the data on reported rabies cases can be quite valuable. Johnson (1966:25) stated that the "statistics on rabies by county offers one method of illustrating the ecology of rabies in wildlife." Even incomplete data reveal which of several possible wildlife species is the major victim of clinical rabies within the reporting area. Data on reported cases may also help to clarify the geographical extent of the rabies problem within the area.

Records covering many years may be valuable in determining the distribution of the disease among several counties, severity of outbreaks, seasonal trends, relative abundance between years, and annual endemicity (Wood 1954:132).

It is very likely that the number of rabies cases reported by local health departments reflects only a small percentage of the wild animals which actually die of rabies. Linhart (1960:4-5) believed that the percentage of rabid foxes in New York submitted for diagnosis ranged from 1 to 10 percent of the total which actually developed the disease. In Florida, Jennings et al. (1960:177) stated that, in general, between 6 and 15 percent of the gray foxes which actually died of rabies were reported. Sikes (1970:9) believed that at most only about 10 percent of rabid wildlife are reported. However, in areas with a moderate human population density, it seems unlikely that a wildlife rabies problem could exist without some official recognition. Jennings et al. (1960:178) thought that enzootic rabies in a gray fox population could not exist in a thickly settled county without producing some reported cases.

The duration of a rabies epizootic can be highly variable. In Florida a fox rabies epizootic lasted from 1953 to 1958, but most of the 13 counties involved reported cases from only two consecutive years (Jennings et al. 1960: 173). A skunk rabies epizootic lasted from 1907 to 1910 in Arizona (Johnson 1965:830). Several localized raccoon rabies epizootics in Florida lasted less than a year (Bigler et al. 1973:330-332). In Virginia fox rabies epizootic lasted from 25 to 60 months (Carey 1974:51).

Rabies epizootics usually have a relatively distinct termination at which time the disease either disappears from the area or the enzootic condition becomes evident. Some authors believe that epizootics "burn themselves out" when the density of the host population reaches a level which is too low to sustain large scale transmission (Marx and Swink 1963:172, Frank 1972:80). However, in northern Florida rabies persisted longer in areas of moderate fox population densities than in areas with abundant foxes (Jennings et al. 1960:177).

Rabies outbreaks may have a devastating effect on wildlife populations. In Europe an estimated 50 percent of all the foxes in a given area may die of rabies during an epizootic (WHO 1970:48). Johnson (1960:273) stated that rabies may have exterminated the coyote (Canis latrans) in certain regions of California and Oregon during a 1910-1915 outbreak. Skunks were virtually eliminated on a 130 ha (320 acre) area in Wisconsin due to rabies in combination with trapping (Parker 1962:275). Among foxes in North America rabies outbreaks can produce "rapid die-offs" (Johnson 1971:239), and may reduce the population to a very low level (Johnston and Beauregard 1969:368).

Many infectious diseases seem to occur only in areas with a distinct set of environmental conditions. Pavlovsky (1969:9) referred to these areas with a characteristic climate, vegetation, and soil as the natural nidi of their respective diseases. Nidus, in this context, refers to the place where a disease exists, and the term is synonymous with focus which is commonly used in the United States. A review of the concepts regarding disease nidality is given by Carey (1974:15-22).

Within the United States wildlife rabies cases do not appear to occur randomly in space. Rabies cases in the various wildlife hosts are likely to occur in distinct foci. In a general sense, the limitation of rabies infection to only a part of a species range is an example of the focal nature of rabies. The striped skunk inhabits most of the continental United States, but reported skunk rabies cases are most prevalent in California and the central United States (USDHEW 1976a, USDHEW 1976b). The same situation can be seen in the concentration of raccoon rabies to those populations of the species in the southeastern United States.

While wildlife rabies may be a problem over large areas such as the Great Plains and Europe (Winkler 1975:6-9), reported rabies cases are often restricted to a single county or several counties (Sikes 1970:4). Davis and Wood (1959: 117) noted that "rabies occurs at a high prevalence in a few small areas." Scholtens and Tierkel (1963:53) stated that rabies epizootics are "extremely localized affairs" which must represent numerous nidi of infection. Bigler et al. (1973:327) reported that raccoon rabies in Florida occurred within "relatively localized epizootics." In Alaska most of the recorded rabies outbreaks have been limited in geographical extent (Rausch 1958:258). Serokowa (1968:66) showed that wildlife rabies in Poland was limited to several stationary foci.

However, other studies have presented data which show that rabies cases can occur without any geographical pattern. Verts (1967:172) reported that many rabid skunks were distributed sporadically in space. Jennings et al. (1960:171) observed that there was no apparent relationship in space among the fox rabies cases reported in the years preceding a large fox rabies epizootic. In analyzing 14 years of striped skunk rabies data in North Dakota, Rakowski and Andrews (1972:70) concluded that the current methods of data collection were inadequate to detect "any foci of rabies, and offer no definite proof that such centers of infection exist."

Several studies have reported that the sites of new rabies cases appear to radiate from the areas of older enzootic or epizootic rabies situations. In Europe wildlife rabies has spread widely from what was believed to be its original focus in the former Polish Corridor (WHO 1970:48, Winkler 1975:6-9). Bigler et al. (1973:327) noted that raccoon rabies in Florida was first reported along the central east coast in 1947 and then seemed to spread north and south along major waterways. Sylvatic rabies in Virginia appeared to move from county to county in a rather predictable pattern based on the spread of the disease toward areas of wildlife overpopulation (Marx and Swink 1963:172), but several other complex factors may also influence the spread of fox rabies (Carey 1974:88-104). A fox rabies epizootic in northern Florida spread rapidly from county to county, but this movement was impeded to a degree by the major river systems which appeared to act as barriers (Jennings et al. 1960:176).

Some studies have examined areas with a wildlife rabies problem in an effort to determine the landscape epizootiology of the disease. In certain situations the geographical distribution of reported rabies cases can be explained by the presence of a large, rabies conscious human population (Rakowski and Andrews 1972:66) or the presence of habitat suited to the overpopulation of the host species (Toro 1966:132, Marx and Swink 1963:171). Lewis (1972:248) determined statistically that reported cases of skunk rabies in Oklahoma were associated with neither human population nor habitat diversity. Davis (1974:80) observed that fox rabies cases in Georgia were very numerous during a period when abandoned croplands provided excellent habitat for foxes, and as this land became forested the level of fox rabies declined. Fredrickson and Thomas (1965:495) suggested that fox rabies areas in Tennessee appear to be associated with areas having caves which may harbor rabid bats, a possible source of rabies infection for terrestrial wildlife. In Virginia, Carey (1974:64) noted that most fox rabies cases occurred within the part of the state designated as the Alleghanian Biotic Region, and that the counties with an epizootic rabies problem formed a portion of this Region and were generally limited to counties in the Ridge and Valley Provinces which had less than 74 percent forested land. Scatterday et al. (1960:949) reported that in Florida sporadic fox rabies cases occurred in the peninsular counties which are distinct in geography, ecology, and economy from the panhandle region where several epizootics have occurred. Several localized epizootics of raccoon rabies in Florida were associated with human activity and major destruction of wildlife habitat which forced the raccoon population into unnatural habitats (Bigler et al. 1973:334).

Like the cyclic fluctuations of many animal populations, the occurrence of rabies cases in some regions may reach high levels at intervals which vary from a few years to a century. Johnson (1965:814) suggested that the rabies epidemic of the mid-1960's was worldwide and similar in nature to a rabies upsurge 100 years ago. Johnston and Beauregard (1969:367) noted a distinct three-year cyclic peak in red fox rabies in Ontario, and stated that this phenomenon was also present in Europe. Friend (1968:82) observed that periodic fluctuations among foxes in New York seemed to occur at five-year intervals. Cyclic peaks have not been reported for rabid skunks, but Tierkel (1959:197) postulated that in the past skunk rabies probably occurred in waves which were related to cyclic fluctuations of skunk populations. In Ontario skunk rabies cases from 1963 through 1972 showed no evidence of a three to five-year cycle (Webster et al. 1974: 166).

There are more data concerning the occurrence of annual cycles in the level of reported wildlife rabies. Rabies cases among foxes are not distributed uniformly during the year (Friend 1968:82, Johnston and Beauregard 1969:360, Prior 1969:26, Schnurrenberger et al. 1970a:1332). The occurrence of an annual peak or peaks in the incidence of skunk rabies has also been observed. In Illinois skunk rabies cases are most numerous during the March-July period (Verts 1967:162, Schnurrenberger et al. 1970b:1338). Skunk rabies cases in Ontario appeared to peak in December (Johnston and Beauregard 1969:360), and Webster et al. (1974:164) added that in December peak was followed by a smaller peak in April. Skunk rabies cases in New York showed a high point in April and a lesser peak in October (Friend 1968:88). Parker (1962: 276) noted that skunk rabies in the north-central states occurred primarily from January through July with peaks in April and July. A peak in wildlife rabies cases in the spring is generally considered to be the result of the stress and intraspecific conflict of reproduction (Friend 1968:82). A smaller peak in the fall, if it occurs, is believed to be the result of stress and contact during the dispersal of juvenile skunks with the accompanying intraspecific conflict (Webster et al. 1974:165).

A crucial problem in rabies ecology is determining the species or group of species which serve as a reservoir for the rabies virus. A tentative axiom in the epizooticlogy of some viral diseases is that the apparent host species, the species experiencing overt illness, is not the reservoir species. This concept postulates that the disease agent is circulated harmlessly in a well balanced host-parasite system among members of the reservoir species, and it is only chance infections of individuals in nonadapted species which result in clinical disease. This principle may or may not apply to wildlife rabies. The appearance of a rabies outbreak in an area after an extended period without any reported rabies cases usually cannot be completely explained (Johnson 1971:249).

In North America insectivorous bats have been mentioned as a possible reservoir and rabies source for terrestrial wildlife (Jennings et al. 1960:171, Fredrickson and Thomas 1965:495, Gunson and Schowalter 1974:3). However, the ability of rabies infected bats to naturally infect terrestrial carnivores is still uncertain (Constantine 1971: 257), and several authors have expressed doubt that bats serve as a rabies reservoir for the major rabies hosts (Baer and Adams 1970:644, Johnson 1971:244). In a recent review of rabies among nonhematophagus bats, Baer (1975:92) stated that there "is evidence both for and against insectivorous bats being involved in transmission of the disease to wildlife."

There is also the possibility that a species or group of species which are seldom, if ever, reported as rabid may constitute an inapparent rabies reservoir. In Florida researchers concluded that an inapparent rabies reservoir among the wildlife of the area was possible (Scatterday et al. 1960:950, Jennings et al. 1960:171). Rodents are capable of developing clinical rabies, but they do not appear to play a role in the maintenance of the disease in the major host species (Winkler 1972b:566). Johnson (1966: 29) stated that the weasels (*Mustela* spp.) are present in all known foci of enzootic rabies in North America, and this group of animals may be involved in the maintenance of the rabies virus despite their low numbers among recorded rabies cases. Because there is no evidence of rabies epizootics among weasels, they fit the theoretical characteristics of a reservoir species (Johnson 1971:243).

In addition to the concept of a multi-species complex for the maintenance of wildlife rabies as expressed by the reservoir species-to-host species idea, it is possible that the virus is carried continuously within the major apparent host species. In the United States the maintenance of the rabies virus within populations of recognized host species has been suggested for the raccoon (Bigler et al. 1973:333, McLean 1975:75) and the striped skunk (Verts 1967:174-176, Sanderson et al. 1967:92). Carey (1974:144) suggested that a balanced host-parasite relationship might exist between the rabies virus and some gray foxes in Virginia.

In considering the concept of a single reservoir/host species, it is necessary to explain methods which would permit the continual circulation of the virus during those periods when reported cases are rare or nonexistent. While it is certainly possible for rabies to be maintained in a species by the classical biting mode of transmission without reported cases, it is also conceivable that some biological reservoir mechanism permits infection and subsequent transmission in the absence of clinical disease. McLean (1975:75) stated that experimental and field data on raccoon rabies in Florida "support the concept of sublethal infection." He added that the precise mechanism for the establishment of such chronic, latent infections is unknown, but such factors as (1) low quantity of virus in the inoculum, (2) low virulent component of the virus gene pool, and/or (3) transmission by nonbite routes such as urine might be involved.

If latent rabies infections do exist in members of the major host species, the factor or factors which can reactivate the virus and trigger the beginning of the incubation period leading to the clinical disease are important aspects in rabies ecology. One of the most commonly implicated factors is stress. Soave (1964:269) associated the reactivation of rabies in a laboratory guinea pig (*Cavia cobaya*) with the stress of overcrowding. In striped skunks reactivation may be the result of any unusual stress such as malnutrition during winter or reproduction and lactation in females (Verts 1967:175). Physiologic changes during the breeding season and stress could reactivate chronic, latent rabies infections in raccoons (McLean 1975:75). Among bats rabies mortality appears to increase during migration (Constantine 1967b:883). Among foxes the effects of the fall dispersal on juvenile males could account for the increased level of rabies in that segment of the population (Johnston and Beauregard 1969:367). The stress of long captivity was implicated in the reactivation of rabies after 209 days in a bat (*Eptesicus fuscus*) (Moore and Raymond 1970:167-168).

While large-scale outbreaks of some infectious viral diseases can be linked to abnormally high population levels of the host species, the relationship between the stresses of overpopulation and the occurrence of rabies is complex and not completely understood. Wildlife rabies is generally considered to be a density dependent disease (Verts 1967:153, Linhart 1960:5). Epizootics of raccoon rabies in Florida seemed to occur during periods of abnormally high population levels (Frank 1972:82, McLean 1975:68). Several studies have reported that fox rabies outbreaks occurred during times of high densities in fox populations (Rausch 1958:

255, Marx and Swink 1963:172, Johnson 1971:238-239). Rabies cases among arctic foxes (<u>Alopex lagopus</u>) has usually been associated with large numbers of foxes and years of marked migrations (Crandell 1975:35).

However, the occurrence of wildlife rabies does not appear to be completely dictated by population levels of the host species. Winkler (1975:18) remarked that the difficulty of obtaining absolute census data on fox populations makes it difficult to affix exact values to the relationship between host density and epizootic potential. Parker et al. (1957:226) found much higher population levels of foxes in areas free of fox rabies than in areas with fox rabies. The presence or absence of wildlife rabies in a particular area is probably related to many factors of which high host density may be only one (Wood and Davis 1959:123, McLean 1970:232).

An important aspect of viral disease ecology is the ratio of immune animals to susceptible animals in the population, i.e., the degree of herd immunity (Schwabe et al. 1977:158-160, Fenner and White 1976:191). If rabies is not invariably fatal, a portion of those animals which survive infection may develop an immunity sufficient to resist future infections. Rabies epizootics might be possible only in areas with a certain ratio of susceptible to immune animals (Sikes 1970:10, Everard et al. 1974:195, Carey 1974:144). After a rabies epizootic the population of the host species might contain a high percentage of animals with some degree of immunity. This immune segment of the population could retard or prevent the dissemination of the rabies virus. In time, however, susceptible animals would be added to the population by immigration and reproduction. As these susceptible animals formed a larger portion of the total population, the probability of new rabies cases, the epizootic potential of the population, would increase. Wildlife rabies outbreaks may be more dependent on the immune status of the animals added to the population than the simple increase in host species density.

At the present time effective control of wildlife rabies seems impossible due to the lack of knowledge concerning the epizootiology of the disease. The efforts at reducing the population of the visible host species during an epizootic already in progress may help reduce the incidence of the disease, but such efforts do not seem successful in preventing other outbreaks in subsequent years. When considered from an evolutionary viewpoint, certain population reduction programs might be counterproductive. Carey (1974: 145) noted that foxes which survive a rabies outbreak may have genotypes which are suited to establishing a balanced, subclinical host-parasite relationship with the rabies virus. When viewed from this perspective, he postulated that population

> reduction constantly instituted after the peak of an epizootic could act as a selective pressure against those foxes which resisted the virus, thereby negating the "progress" in the coadaptation of the host and parasite.

The application of elaborate and expensive control procedures during the periods between epizootic which might prevent outbreaks may seem unwarranted to the general public and may, in fact, be nonproductive. Therefore, it would seem that the elucidation of sylvatic rabies ecology should precede or be concurrent with the development of various control procedures. The reservoir mechanism(s), landscape epizootiology, factors initiating outbreaks, and the modes of intra- and interspecific transmission must be determined before any systematic control program for wildlife rabies can be effective.

APPENDIX C

SEROLOGICAL EPIZOOTIOLOGY

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A critical problem in studying infectious diseases in wildlife populations is the fact that diseased animals can rarely be collected in numbers adequate for study during interepizootic periods. In wildlife populations even a slight decrease in fitness caused by a disease agent can result in death. Such factors as starvation and predation often remove diseased animals from the population before clinical signs are apparent, and even the animals dying directly from disease are rapidly consumed by a host of scavengers.

One solution to this problem involves the use of serological surveys within wildlife populations. Serological surveys are projects designed to collect blood samples from members of a population in order to study these samples for evidence of past or present infections and/or physiological condition. Serological surveys were used in the surveillance of domestic animal diseases during the early 1900's (Schwabe et al. 1977:33). Serological surveys for the detection of rabies antibodies in wildlife populations of North America were reported as early as the late 1950's (Tierkel 1959: 197-198).

Serological epidemiology with respect to infectious disease agents rests on the biological principle that when an immunocompetent animal is infected with a particular disease agent, the body will respond by forming specific antibodies against that disease agent. By detecting these specific antibodies against known disease agents, it is possible to discover the immunological "footprints" of an infection in the remote or recent past (Paul and White 1973:16).

The fundamental conclusion which can be made from a rabies serological survey is whether rabies infected animals are present within the wildlife of the area examined. These data are essential in determining the danger of wildlife rabies in the area. McLean (1975:63) noted that serological methods in combination with other data can determine the role of the various wildlife species in the epizootiology of rabies. He also reported that serological data can detect the progression of rabies infections over geographical areas in the absence of reported rabies cases (McLean 1975:65). The comparison of serological data and the level of reported cases may reflect on the validity of the local rabies reporting system (Bigler et al. 1973:333).

Beyond determining the presence or absence of the rabies virus, a multi-species rabies serological survey can aid in determining the epizootiology of the disease. The detection of rabies antibodies in only the visible host species would increase the possibility that the disease is transmitted intraspecially and that the visible host species and reservoir species were one and the same. On the other hand, the presence of antibodies in a large percentage of several wildlife species would suggest that exposure might occur interspecifically, and that the reservoir species was one or several of the species tested. A thorough investigation might determine the role of transient groups of animals such as bats in the spread of rabies.

Some multi-species serological surveys among terrestrial wildlife in North America have found rabies antibodies in several, but not a majority, of the species tested. Sikes (1962:1047) found rabies antibodies in two of five species trapped in Alabama. In Illinois Verts (1967:157) detected significant levels of rabies antibodies in three of six species. In Tennessee Mahon (1973:82) found two of seven species to have seropositive members. However, other studies found rabies antibodies among members of all or most of the species tested. In Iowa Niemeyer (1973:14) reported rabies seropositive animals from four of the four species tested. In Florida rabies antibodies were found in two of the three species tested (Bigler et al. 1973:329-330). The results of these serological surveys must take into account that some animals may be infected with rabies and even develop clinical rabies without forming rabies antibodies (Sikes 1962:1043-1047). At the present time, therefore, the available data do not permit the differentiation of terrestrial wildlife species into strict categories of reservoir species and host species.

Another important use of serological epizootiology in wildlife rabies research involves the comparison of the level of rabies seropositive animals between several different areas. If sampling can be done more or less randomly over a large area, it might be possible to determine whether rabies infected animals were randomly distributed within the area or concentrated in localized foci or even a single focal area. The determination of which pattern existed in a given region would have significant epizootiological and control implications. If rabies seropositive animals were distributed randomly over a large area, then control measures should not be localized, and health officials would have to realize that rabies infected animals might move into the area of the control effort from adjacent areas. If, on the other hand, rabies seropositive were concentrated in distinct foci, localized control measures might be more productive. It would also be feasible to search for environmental factors or population characteristics which were unique to the focal areas. Despite the obstacles involved in establishing significant environmental relationships, the determination of any factor which was highly characteristic of the areas having a high percentage of rabies seropositive could help to establish the landscape epizootiology of rabies in the region. If such factors existed, their elimination, alteration, or neutralization could greatly reduce the incidence of rabies.

In human epidemiology the periodical use of serological surveys is an important feature in controlling disease (Melnick 1973:153). In a rabies control program the periodical sampling of the same population, and ideally the same individuals, could greatly improve rabies control. Such sampling might reveal the initial arrival or return of rabies infected animals into the area. The detection of an increase in the prevalence of rabies seropositive animals within a population over a period of time might permit the forecasting of rabies epizootics (Tierkel 1959:198). Any data which would enable control operations to begin prior to a rabies outbreak are of great value in reducing the threat of the disease and the cost of controlling it.

Serological epidemiology is also aimed at determining which segments of a population may have a greater exposure rate (Paul and White 1973:18). In epizootiological studies this effort is directed toward the detection of any particular sex or age class which may have significantly high or low percentages of seropositive animals. Bigler et al. (1973: 334) found that adult female raccoons had a higher rabies infection rate than males and suggested that there might be some sexual differentiation in infection. Niemeyer (1973: 17) found a greater percentage of female raccoons to be rabies seropositive. While no conclusive explanation is currently available for these data, such information may provide a clue to the mechanism whereby the rabies virus is maintained and transmitted within the population.

In some cases the significance of the presence or absence of rabies seropositive animals in a wildlife population may be unclear (Verts 1967:148). However, some conclusions based on serological surveys are possible. The presence of rabies seropositive animals in a given area strongly suggests that the rabies virus is being circulated in that area. The presence of rabies seropositive animals suggests that a certain number of wild animals can be exposed to the rabies virus without developing the clinical disease (Sikes 1962:1047). This type of investigation may show that a portion of several wildlife species, both the common hosts and those rarely involved in reported cases, are exposed to rabies in their natural habitat. The technique of serological epizootiology has been used to probe the ecology of wildlife rabies only in recent years, but it is certainly a valuable research tool and should play an ever increasing role in all phases of wildlife disease work.

APPENDIX D

STRIPED SKUNK ECOLOGY

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STRIPED SKUNK ECOLOGY

Both the striped skunk and the spotted skunk are found in Tennessee. The spotted skunk is commonly referred to as the "civet cat," and the term skunk usually means the striped skunk. In an early game survey of northeastern Tennessee, Wing (1940:311) mentioned that both the "common" skunk and the spotted skunk were present in the area. Linzey and Linzey (1971:66) stated that the spotted skunk often occupies the same area of the Great Smoky Mountains National Park as the striped skunk, but the latter is more common. Smith et al. (1974:92) found the spotted skunk to be rare in northeastern Tennessee and generally more numerous at elevations over 1200 m. In east-central Tennessee, Mahon (1973: 76) captured 43 striped skunks and two spotted skunks.

In the United States most skunk rabies cases occur among striped skunks (Parker 1975:44). During 1974 there were 1,429 reported cases of skunk rabies in the United States, and of this total 1,146 cases (80 percent) were among striped skunks, five cases (1 percent) were among spotted skunks, and 278 cases (19 percent) were among unspecified skunks (USDHEW 1976a:8). Despite the lack of knowledge concerning the relative epizootiological importance of rabies among the two skunk species in Tennessee, the striped skunk is the most common skunk and a frequent rabies host in the state, and this species was considered the major target of this investigation.

The striped skunk is a very adaptable animal and can live in a variety of environments (Parker 1962:274). Verts (1967:79-83) stated that while woodlots can be important as striped skunk habitat, the highest populations of the species in northwestern Illinois were found in more open country such as cornfields and fencerows bordering cultivated areas. The preference of striped skunks for open habitats was noted by Stout and Sonenshine (1974b:144) in Virginia and Shirer and Fitch (1970:493) in Kansas. Niemeyer (1973:19) captured few striped skunks in wooded areas. He found skunks most frequently in agricultural areas, near farm buildings, and in urban areas. Striped skunks prefer areas near water and are common in pastures and grasslands along streams (Andrews and Ferris 1966:132).

Striped skunks are omnivorous in their feeding behavior. Verts (1967:69) summarized the data on the food items used by skunks and noted that insects are the primary food with small mammals, plant materials, and other vertebrates being included in the diet. Skunks seem to be opportunistic feeders with availability playing a large role in their choice of food (Verts 1967:74).

Striped skunks apparently do not live long in the wild. While some may live three to five years in captivity, Verts

(1967:116) reported that the age of the oldest tagged skunk recaptured in Illinois was 3.5 years old. He also noted that the generally short life span indicates a high mortality rate which results in the complete replacement of the skunk population in a relatively short time. Linduska (1947:128) reported that only one of 115 striped skunks trapped on an area in Michigan was known to still be in the area more than two years after initial capture. Stout and Sonenshine (1974b:143) recaptured one female striped skunk over a 48 month period, but the average time between first and last capture for other skunks was 2.7 months. In a northwestern Ohio marsh, 71 percent of the striped skunk population was composed of animals less than one year old with the oldest known member being approximately two years old (Bailey 1971: 200).

There are indications that population levels of striped skunks may fluctuate widely. Allen and Shapton (1942:66) reported a widespread decline in skunks concurrent with an undetermined illness. Parker (1962:278) observed that a sharp increase in skunk rabies cases occurred shortly after a decrease in the harvest of skunks, and he noted the apparent disappearance of skunks in the area after several years of sporadic skunk rabies cases (Parker 1962:275). Verts (1967: 84) cited several studies which suggested that skunk population levels fluctuate greatly from year to year. Stout and Sonenshine (1974b:143) found a steady decline in skunk densities from 1 per 20 ha in the 1963-1965 period to 1 per 40 ha in the 1966-1969 period, but they could find no apparent reason for the decrease. However, on a large South Carolina study area, Wood and Odum (1964:544) found striped skunks to maintain a low but relatively uniform population level.

Data on the population densities of striped skunks show much variation. Verts (1967:85) found the density of striped skunks (based on capture-recapture) to range from 1 per 29 ha to 1 per 7 ha. Allen and Shapton (1942:65) estimated skunk density to be one skunk per 20 ha, and Ferris and Andrews (1967:4) calculated skunk densities which ranged from 1 per 9 ha to 1 per 4 ha. On accessible land on an Ohio marsh, there was approximately one skunk per 12 ha (Bailey 1971:200). In Iowa Niemeyer (1973:33) reported the average density of striped skunks to be 1 per 63 ha.

Verts (1967:86-87) noted that striped skunks appear to live in a clumped distribution pattern rather than being evenly distributed over a given area. Within an area some male striped skunks appear to have distinct home ranges through which females and transient may travel (Bailey 1971: 203). Striped skunks are not generally considered to be territorial (Shirer and Fitch 1970:499), and Bailey (1971: 203) saw no evidence of conflict between adult males and suggested that some type of mutual avoidance may exist among striped skunks.

Striped skunks are active primarily at night and rest in dens or retreats during the day. A single skunk may use several different dens during the warmer months, but restricts its activity to only a few dens during the fall and winter (Storm 1972:35). While dens are commonly above ground in the spring and summer, underground burrows are used in the late fall and winter (Storm 1972:43).

The time spent and distance travelled by skunks on their nocturnal forays depend on the time of year, quality of the habitat, and the sex and age of the animal. Niemeyer (1973:25-26) found that adult striped skunks usually restricted their movements to a maximum of 1200 m from the initial point of capture. Adult skunks may travel approximately 0.8 to 1.6 km per night (Storm 1972:33, Dean 1965: 674). Adult males may travel farther than females (Verts 1967:57-58), and juveniles in the fall probably move less than 0.8 km each night (Verts 1967:50-52).

Despite the fact that striped skunks appear to spend much of their lives within relatively small areas (Verts 1967:61), some individuals may make long movements over extended periods of time. Verts (1967:60) reported the recapture of an adult male after 848 days at a point 9.6 km from a previous capture site.

While skunks may change their den site frequently, they often show a strong attraction for a particular hunting ground (Verts 1967:51). The home range utilized by skunks may vary in size. The average home range of 13 skunks in

Illinois was 9.5 ha (Andrews and Ferris 1966:132). In Ohio the home range of striped skunks ranged in size from 12.5 ha to 46.1 ha with an average of 30.4 ha (Bailey 1971:203).

While the time at which various events in the annual life cycle of the striped skunk occur is different in various parts of the country, the basic outline is clear. The breeding season is in the spring, generally between mid-February and mid-March (Verts 1967:106-110, Bailey 1971:198). Males may mate with several females (Verts 1967:37). After mating, females will chase away the males, and the males play no role in the rearing of the young (Verts 1967:40). The young are usually born in late April or early May (Verts 1967:60), and the average litter size is approximately six or seven young (Verts 1967:112, Bailey 1971:198, Niemeyer 1973:36). The young stay with the mother until they are about 2.5 to 3 months of age and become self-sufficient about August (Verts 1967:47-48, Bailey 1971:199).

Striped skunks do not hibernate, but they do remain in their winter dens for extended periods of time (Shirer and Fitch 1970:494, Sunquist 1974:443). It is not unusual for several skunks to use the same winter den, and as many as six skunks have been found living communally in one den (Houseknecht 1969:304, Sunquist 1974:438). The winter denning period can be a time of severe stress, and skunks can lose 55 to 65 percent of their fall weights (Houseknecht 1969:304). Skunks may also share a winter den with other species such as the opossum (Shirer and Fitch 1970:501). Occasionally skunks in winter dens are disturbed by predators such as the red fox (Sunquist 1974:438). The potential for disease transmission during both intra- and interspecific encounters in winter dens is considerable. Skunks may leave their dens about March in response to hunger or breeding impulses (Sunquist 1974:442).

At the present time the striped skunk plays a significant role in the rabies problem of the United States. Skunks are a major source of rabies infection for humans (Hattwick et al. 1973:1080). During 1975 rabid skunks were reported from 32 states (USDHEW 1976b:1). Efforts at determining the best approach for controlling skunk rabies are being undertaken in both the laboratory and in the field. There are data to indicate that striped skunks can react in a variety of ways to rabies infection (Table 49). Skunks can apparently survive infection with or without producing serum neutralizing antibodies, and antibodies may or may not be present in skunks which develop clinical rabies. The most important point is that a portion of the skunks within a natural population may be able to survive a rabies infection. With this fact in mind, the disease ecologist should study natural skunk populations and seek to establish the ecological factors which may influence resistance. Field studies have sampled striped populations in the wild in order to locate rabies seropositive animals (Table 50). These studies have shown that between

Table 49. Laboratory studies on the antibody response of striped skunks to rabies virus inoculation.

Mode of inoculation	Dose	Number of skunks: Tested	Developed rabies	Formed antibodies	Source
Bite of rabid bat	*	2	0	0	Constantine and Woodall 1966:26
IM	600 MLD_{50}	2	0	0	" :29
IM	6,000 MLD_{50}	2	1	0	" :29
Bite of rabid bat	*	2	0	1	" :28,30
IM	140-140,000 MLD_{50}	12	*	1[a]	Sikes 1962:1045-1046
IM	20,000 $MILD_{50}$	2	0	0	Parker and Sikes 1966:943
IM	20,000 $MILD_{50}$	14	14	7	"

[a]Skunk died of rabies.

*Data not available.

IM = Intramuscular

MLD_{50} = 50 percent mouse lethal dose.

$MILD_{50}$ = 50 percent mouse intracerebral lethal dose.

Table 50. Skunks with rabies serum neutralizing antibodies in natural populations.

Area	Number of skunks: Tested	Number of skunks: Sero-positive	Percentage seropositive	Source
Areas with a recent history of fox rabies outbreaks	48[a]	7	14.5	Tierkel 1959:198
Alabama				
fox epizootic area	53[a]	0	0	Sikes 1962: 1047
fox enzootic area	35[a]	0	0	"
rabies-free area	12[a]	0	0	"
Illinois	120[b]	2	1.7	Verts 1967: 157
Arizona	200[b]	13	6.5	USDHEW 1971
Florida	58[b]	2	3.4	Bigler et al. 1973: 330
Tennessee	41[b]	1	2.4	Mahon 1973: 82
Iowa				
striped skunk	82	45	54.9	Niemeyer 1973:14
spotted skunk	19	5	26.3	"

[a]Species composition of skunks not given.

[b]Sample contained only striped skunks.

0 and 55 percent of a skunk population may be animals with prior exposure to the rabies virus. A combined effort of detailed field studies and extensive laboratory examination of material collected from wild populations may ultimately clarify the epizootiology of skunk rabies. Such clarification is certainly a logical first step toward control or elimination of rabies among striped skunks.

APPENDIX E

OPOSSUM ECOLOGY

APPENDIX E

OPOSSUM ECOLOGY

The opossum is a very common mammal in Tennessee. The species was noted as a member of the east Tennessee fauna by Wing (1940:311). The species is known to range throughout the Great Smoky Mountains National Park, but it is not common at the higher elevations (Linzey and Linzey 1971:3-4).

The opossum can inhabit a wide variety of environments. Opossums do seem to prefer woodland areas (Fitch and Sandidge 1953:312, Linzey and Linzey 1971:4). In Virginia Stout and Sonenshine (1974a:238) found that opossum population densities were highest in forested, non-agricultural areas and more moderate on agricultural lands. Llewellyn and Dale (1964:121) reported that opossums in Maryland appeared to prefer low, dense woodlands near water with open areas and cultivated land being the least suitable. Opossums can live in cultivated areas (Verts 1963:127). Niemeyer (1973:19) found opossums more frequently in agricultural and suburban areas than in wooded areas of Iowa.

Opossums are omnivorous in their feeding habits and consume a wide variety of food items. In general, opossums eat insects, reptiles, cultivated grains and seeds, fruit, birds, bird eggs, and a host of other plant and animal food items (Reynolds 1945:370-371, Wiseman and Hendrickson 1950:

335). Opossums may eat carrion (Reynolds 1945:369, Lowery 1974:60). Lay (1942:158) remarked that an opossum population would rarely be limited by a shortage of food due to the great diversity of their diet.

Lay (1942:152) noted that opossums apparently do not live long in the wild. He stated that during 24 months of trapping only one of the 59 recaptured opossums was retrapped at an interval exceeding 11 months, and concluded that there was a rapid disappearance of young opossums after weaning which suggested a relatively short life span (Lay 1942:158). In Maryland an adult male was considered to be 36 months old when last trapped, and a female was thought to be 27 months old when last captured (Llewellyn and Dale 1964:115). Based on retrap data in Virginia, Stout and Sonenshine (1974a:241) found that females had a greater mean longevity (3.1 months) than males (2.0 months), and they postulated that the rapid turnover of the opossum population may have resulted from emigration. Data indicate that few opossums survive more than two years, and only 16 percent of the opossums captured as juveniles can be accounted for after six months (Llewellyn and Dale 1964:117).

In favorable areas opossums are able to live at relatively high population densities. This ability may be due, in part, to their almost unrestricted diet and wide choice of nesting sites. Studies have estimated opossum population densities to be 1 per 1.2 ha (Holmes and Sanderson 1965:290), 1 per 1.6 ha (Lay 1942:151), 1 per 8 ha (Fitch and Sandidge 1953:334-335), 1 per 20 ha (Stout and Sonenshine 1974a:238), 1 per 26 ha (Verts 1963:128), and 1 per 65 ha (Niemeyer 1973:33).

Opossums may have relatively stable populations due to omnivorous diet and large reproductive capacity. Stout and Sonenshine (1974a:238-239) did note two periods of above average population density during their six-year study in Virginia, but "the trend was for regular oscillations during the years of the study." Sanderson (1961:26) found a shift in the calculated population density from 112 opossums per km^2 during 1957 to 90 per km^2 during 1958. In certain areas, especially in marginal habitats, severe winter weather may cause widespread mortality (Holmes and Sanderson 1965:290). There may be a 50 percent drop in population density during the winter in some populations (Fitch and Sandidge 1953:334-335).

In general, opossums appear to den and feed alone, but are tolerant of neighboring opossums (Lay 1942:149). Opossums may have a well-defined home range in certain circumstances (Holmes and Sanderson 1965:293), but other evidence suggests that the home range of the opossum is extremely fluid (Fitch and Shirer 1970:178) and not highly developed (Llewellyn and Dale 1964:116). There appears to be a great deal of overlap among opossum home ranges (Fitch and Shirer 1970:174) as well as a large number of itinerant opossums within a given area

(Lay 1942:149, Llewellyn and Dale 1964:116). The opossum is not a territorial animal in the sense of vigorously defending a particular area (Fitch and Sandidge 1953:316). Shirer and Fitch (1970:499) estimated the "minimum home range" of opossums to range from 2.2 ha for a subadult male to 66.5 ha for an adult male. The home range of the opossum has been reported to be 38.8 ha (Verts 1963:128), 14.2 ha (Andrews and Ferris 1966:132), 20 ha or less (Fitch and Sandidge 1953:319), and 4.6 ha (Lay 1942:148). Males and females do not seem to occupy home ranges of significantly different size (Fitch and Shirer 1970:182).

Opossums do not seem to wander widely during their lives (Llewellyn and Dale 1964:118). Holmes and Sanderson (1965:295) found that some opossums stayed in the general area of their birth. Wiseman and Hendrickson (1950:336) indicated a yearly mobility of between 0.4 km and 0.8 km. Niemeyer (1973:26) reported that most adult opossums ranged less than 1.2 km from their initial point of capture. Some opossums do seem to move considerable distances. One opossum was retrapped 11.3 km from a prior release point (Reynolds 1945:375). Young opossums, especially males, may wander widely and settle in areas far removed from their places of birth (Fitch and Sandidge 1953:321, Fitch and Shirer 1970:179), and such immigration into recently depopulated areas may aid in returning opossum populations to normal levels (Holmes and Sanderson 1965:290).

Opossums do not hibernate during the winter, but remain in dens for extended periods of time during harsh weather (Reynolds 1945:376, Shirer and Fitch 1970:494). Winter is a time of hardship for opossums, and periods of severe cold result in long periods between feeding (Fitch and Sandidge 1953:327). Many opossums are in critical condition by spring (Fitch and Shirer 1970:182).

Opossums use a variety of den sites during the year, but in the winter they prefer straw stacks or underground dens (Wiseman and Hendrickson 1950:332). Reynolds (1945:374) reported multiple occupancy of a single den by opossums of the same sex, but no association with other species. However, Shirer and Fitch (1970:501) found dens occupied by both male and female opossums as well as simultaneous usage of a den by an opossum and a striped skunk. Often good den sites used by opossums are also used by such animals as the red fox, raccoon, woodchuck, and skunks although the usage may not be concurrent (Fitch and Shirer 1970:174).

The opossum normally produces two litters of young per year, but may occasionally have three (McManus 1974:3). The reproductive activities of opossums usually last from late January and early February until early fall, usually August or September (Llewellyn and Dale 1964:118-119). Fitch and Sandidge (1953:328-329) noted two breeding seasons among opossums in Kansas with the first litter usually born in March and the second litter coming in June. In Missouri

Reynolds (1945:364) reported that the opossum breeding season lasted approximately from the first of February to the first of September. Most females probably give birth to at least one litter during the breeding season (Holmes and Sanderson 1965:290). Niemeyer (1973:33) found that 85 percent of adult females produced litters. Normally the whole population including young of the preceding year take part in breeding activities during the early spring (Fitch and Sandidge 1953:328). Young opossums remain in the pouch for approximately 90 to 100 days (Lay 1942:154). Those young of the first litter which survive become independent in early summer, usually about late May or early June, and members of the second litter normally become independent in the early fall (Fitch and Sandidge 1953:328-330).

Although opossums, like all mammals, are susceptible to rabies, there seems to be a very low incidence of the disease in the species. The occurrence of rabid opossums appears to be sporadic and there are no confirmed reports of rabies reaching epizootic proportions among opossums. Between 1955 and 1976 the available data show that 39 cases of opossum rabies were reported in the United States (Table 51). The seven rabid opossums in Tennessee were located primarily in middle Tennessee with one case in the northeastern part of the state (Fig. 39).

Laboratory work on opossum rabies has shown that the species is highly refractory to the disease (Beamer et al.

Table 51. Incidence of reported opossum rabies cases in the United States, 1955-1976.

Year	Number of reported cases	Incidence by state
1955	2	Kansas 1, Missouri 1
1956	1	Kentucky
1957	2	Illinois 1, West Virginia 1
1958	2	Missouri 1, Pennsylvania 1
1959	6	Indiana 1, Missouri 1, Nebraska 2, Tennessee 1, Texas 1
1960	3	Kentucky 1, Missouri 1, Nebraska 1
1961	*	
1962	*	
1963	2	Georgia 1, Iowa 1
1964	1	Missouri
1965	6	California 1, Missouri 2, Tennessee 2, Texas 1
1966	2	New York 1, Oklahoma 1
1967	4	Nebraska 1, Tennessee 3
1968	1	Indiana
1969	3	California 1, Texas 1, Virginia 1
1970	1	Florida
1971	2	Tennessee 1, Wisconsin 1
1972	0	
1973	0	
1974	0	
1975	0	
1976	1	Arkansas
Total	39	

*Data not available.

Source: Barr 1963:64 (1955-1960); USDHEW, Center for Disease Control, Zoonosis Surveillance, Rabies (1963-1976).

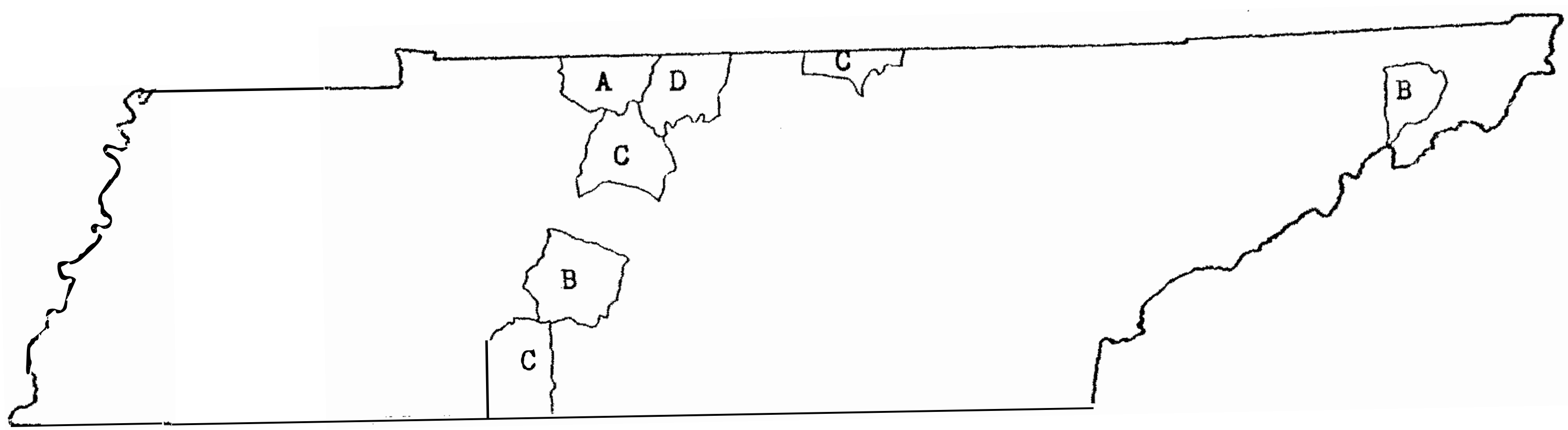


Fig. 39. Opossum rabies in Tennessee, 1946-1976. Map shows the seven counties from which rabid opossums were reported. Letters designate the year in which the case was reported (A:1959, B:1965, C:1967, D:1971).

1960:510, Barr 1963:66-67, Constantine and Woodall 1966:28). Opossums can apparently withstand large inoculations of rabies virus without developing clinical rabies (Beamer et al. 1960:510). Sikes and Tierkel (1962:271) demonstrated that the number of MLD_{50} of a street rabies isolate necessary to kill half the animals in conspecific groups among several species was less than five for foxes, 500 for skunks, 1,000 for raccoons, and over 80,000 for opossums. This resistance of opossums to rabies is considered to be a natural resistance rather than an effective immune response after infection (Barr 1963:66). One point to consider is that the opossum, as a member of the genus *Didelphis*, has a basal metabolic rate which is among the lowest recorded for mammals (McManus 1974: 2), and it has been suggested that a decreased metabolic rate in a rabies host could delay virus propagation and possible increase the chances for survival (Enright et al. 1968:1116). For a short-lived animal such as the opossum, any factor which resulted in an extended incubation period might virtually eliminate the clinical disease in the species.

Opossums which do develop rabies can show both the clinical signs of dumb or furious rabies. Barr (1961:61) stated that rabid opossums in his study showed only the signs of dumb rabies, and showed no tendency to bite or behave aggressively. He also suggested that rabid wild opossums would have only a slight possibility of transmitting the disease to other wild animals. Constantine (1967a:51) reported that two of three opossums which died of rabies showed signs of paralytic, or dumb, rabies and the third demonstrated signs of both furious and paralytic rabies, and he noted (Constantine 1967a:25) that the length of clinical illness, or morbidity duration, among opossums was impressively long.

In addition to their innate resistance, opossums can also produce SN antibodies when infected by the rabies virus. Barr (1961:59-60) demonstrated that three of 17 (17.6 percent) opossums inoculated with rabies virus developed SN antibodies and did not develop clinical rabies. These antibodies were present as early as 39 days post-inoculation and in two cases rabies antibodies were still present at the termination of the study (92 and 98 days post-inoculation). The third opossum had a low rabies antibody titer on post-inoculation day 78 and was seronegative on post-inoculation day 98 (Barr 1961: 81). Of the 14 opossums which did not develop SN antibodies, four developed clinical rabies and 10 remained healthy (Barr 1961:60). He concluded that opossums can resist potentially lethal doses of rabies virus without developing SN antibodies and only a minority of opossums exposed to the virus develop sublethal, immunizing infections.

While less than 20 percent of the opossums exposed to rabies may form SN antibodies, some field studies have found rabies seropositive opossums in wild populations (Table 52). The percentage of rabies seropositive opossums appears to be

Table 52. Opossums with rabies serum neutralizing antibodies in natural populations.

Area	Number of opossums tested	Number of opossums seropositive	Percentage seropositive	Source
Area with a recent history of fox rabies	185	2	1.8	Tierkel 1959:198
Alabama				
fox epizootic area	73	0	0	Sikes 1962: 1047
fox enzootic area	42	0	0	
rabies free area	12	0	0	
Georgia	*	1	*	SCWDS[a] 1967: 54
Illinois	143	0	0	Verts 1967:156
Florida	93	*	1.5	Bigler et al 1973: 329-330
Iowa	84	1	1.2	Niemeyer 1973:14

[a]SCWDS = Southeastern Cooperative Wildlife Disease Study.

*Data not available.

low, and it is possible to conclude that the opossum is not involved in the wildlife rabies cycle (Niemeyer 1973:49). Perhaps for this reason the opossum has been excluded from some rabies field studies. However, it is interesting to note that the opossum fulfills many of the criteria associated with a reservoir species. The species has an innate resistance to the disease, but opossums can conceivably transmit rabies to other animals especially if the several nonbite methods are considered. Therefore, the species which lives in proximity to man and the major rabies hosts should be included in any serological survey aimed at determining the ecology of rabies in wildlife populations.

APPENDIX F

FERAL CAT ECOLOGY

APPENDIX F

FERAL CAT ECOLOGY

The cat (Felis domestica) has always walked a thin line between the role of a dependent house pet and a self-sufficient predator. While the term feral technically means wild, untamed, or savage, the word can be used to refer to those members of domesticated species which feed and reproduce independently of man. Cats are common in many rural areas of Tennessee. While these may be either feral or true house pets, the cats which cannot be assigned to either category may be called free-roaming.

There are very little data on the ecology of feral cats. Andrews and Ferris (1966:132) determined that 23 of 29 cats on their 1,036 ha study area in southeastern Illinois were feral, but they had insufficient data to measure home range size or habitat preferences. However, they noted that the general pattern of cat captures indicated that these cats "preferred open fields, especially those along the major streams, rather than woodlands." Feral cats were trapped on the Savannah River Plant area in South Carolina which was mainly forested with abandoned farmland undergoing succession to woodland (Wood and Odum 1964:544). The presence of feral cats in wooded areas was also noted by Gill (1975:78) and Errington (1936:64). Gill (1975:75) stated that cats may search for prey over distances of 8 to 12 km. The food habits of feral cats are discussed by McMurry and Sperry (1941:186), Toner (1956:119), Coman and Brunner (1972:851), and Doucet (1973:591).

Presumably feral cats are plagued by diseases and parasites similar to those which affect other wild Felidae. From a human perspective one of the most significant diseases of domestic cats is rabies. From the time of the earliest national records in 1953, rabid cats have occurred at a moderate but persistent level (Vaughn 1975:140). From 1953 through 1975 almost 6,000 cases of cat rabies were reported in the United States (USDHEW 1976b:9). During this period the number of reported rabies cases among dogs, foxes, skunks, and bats changed drastically, but the number of rabid cats decreased gradually from 538 cases in 1953 to 104 cases in 1975 (USDHEW 1976b:9).

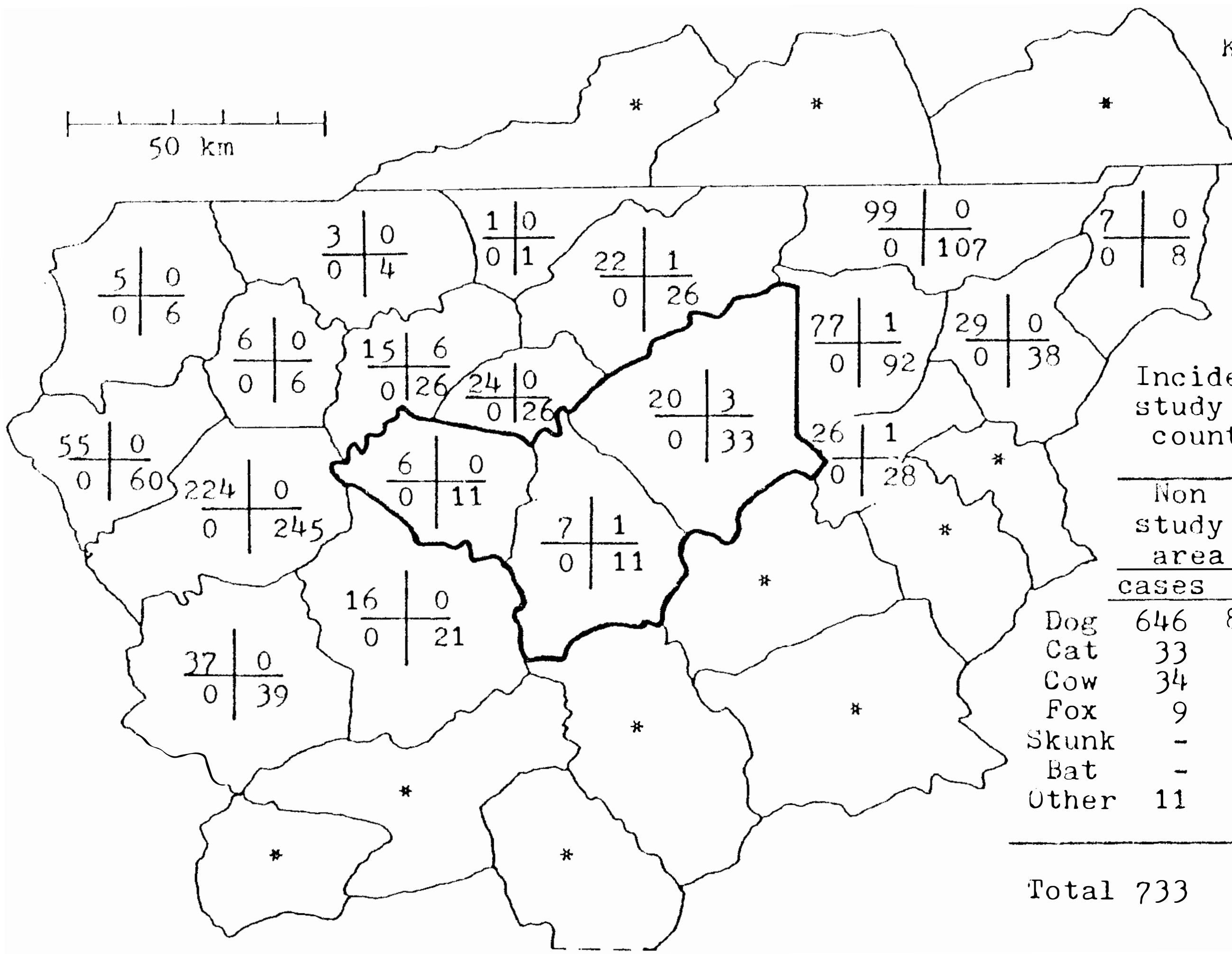
Rabid cats present a significant health hazard to humans (Vaughn 1975:140-141, USDHEW 1976b:2). Prather et al. (1975:48) stated that rabid cats make sudden, unexpected, and unprovoked attacks on people, and these attacks are often from the rear and cause deep puncture wounds. They also noted that rabid cats were involved in multiple human contacts more frequently than dogs (Prather et al. 1975:51). The behavior of rabid cats may vary, but they are usually extremely vicious (Tierkel 1959:187).

Little is known about the epizootiology of cat rabies, and it is often assumed that cats are infected by the most visible rabies host in the area. Cats could also be infected as they prey upon a less visible rabies reservoir species (Vaughn 1975:147-149). Prather et al. (1975:47, 50) noted that cat rabies cases in Florida were more common in the latter half of the year with a peak in November, and they postulated that cat rabies in the summer might be related to rabies cases among bats which also peak during that time. Cat rabies cases usually occur sporadically, but small outbreaks of rabid cats have occurred in Arizona and Maine, presumably as a result of exposure to rabid wildlife (Vaughn 1975:148).

Feral or free-roaming cats seem to be routinely excluded from field studies on wildlife rabies (Mahon 1973: 41,43,76, Niemeyer 1973:12). This may be based on the fact that seropositive cats could have received a rabies vaccination and the rabies antibodies might not reflect the circulation of the virus in the wild. However, Vaughn (1975:140) stated that rabies vaccinations are infrequently used among cats. During 1975 only 33,714 cats were vaccinated against rabies in the state of Tennessee as opposed to 411,515 dogs, and 48 percent of the cat vaccinations occurred in the four counties with large urban populations (Tennessee Department of Public Health 1976:17). Therefore, the average number of cats vaccinated in the other 91 counties was only 190, and these vaccinated cats may not be those free to wander the fields and woods of rural areas. Considering these circumstances, it would seem reasonable to include free-roaming cats captured away from human dwellings in field investigations of wildlife rabies.

APPENDIX G

INCIDENCE OF LABORATORY CONFIRMED RABIES IN THE STUDY REGION, 1946-1976



Key to map symbols

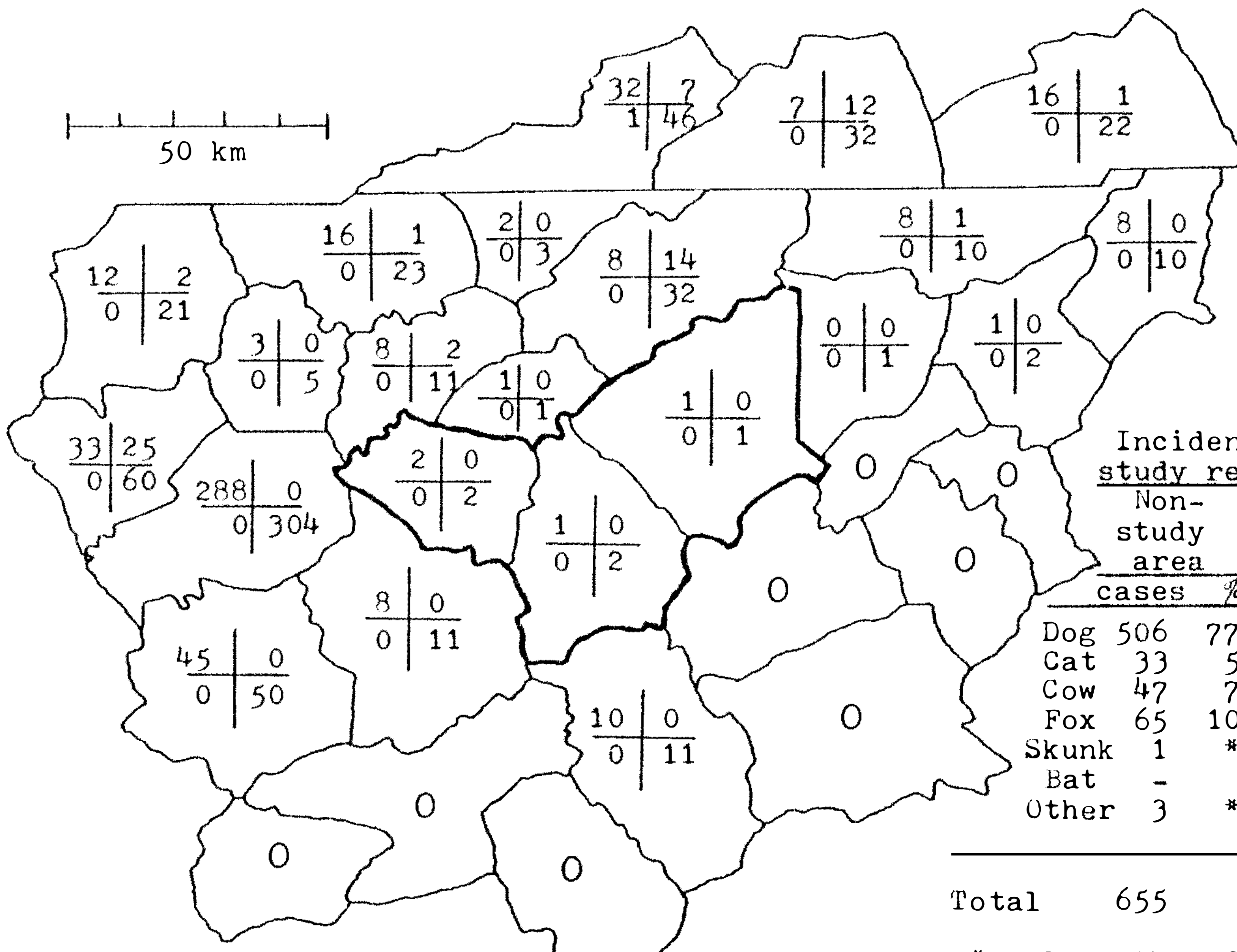
*= data not available

Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

Incidence of rabies in the study region (Tennessee counties only), 1946-1949

	Non study area cases	%	Study area cases	%	Total cases	%
Dog	646	88	33	60	679	86
Cat	33	4	6	11	39	5
Cow	34	5	12	22	46	6
Fox	9	1	4	7	13	2
Skunk	-		-		-	
Bat	-		-		-	
Other	11	2	-		-	
Total	733		55		788	

Fig. 40. Incidence of laboratory confirmed rabies among the major animal categories in the study region (Tennessee counties only), 1946-1949. Three county study area shown in heavy outline.

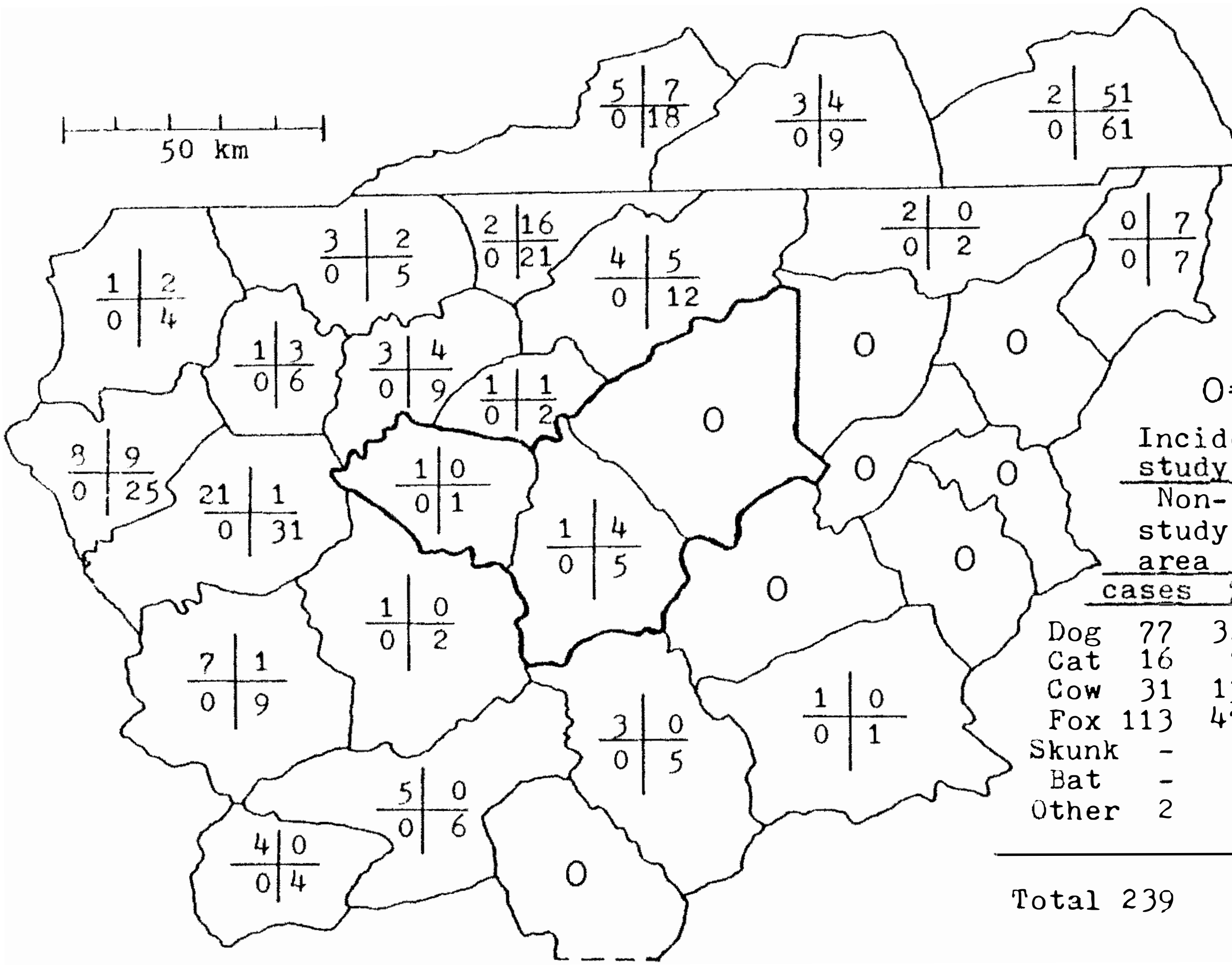


Incidence of rabies in the study region, 1950-1953

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	506	77	4	80	510	77
Cat	33	5	-		33	5
Cow	47	7	1	20	48	7
Fox	65	10	-		65	10
Skunk	1	*	-		1	*
Bat	-		-		-	
Other	3	*	-		3	*
Total	655		5		660	

* = less than 0.5 percent

Fig. 41. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1950-1953. Three county study area shown in heavy outline. North Carolina counties show only 1952-1953. Virginia counties show only 1951-1953.



Key to map symbols

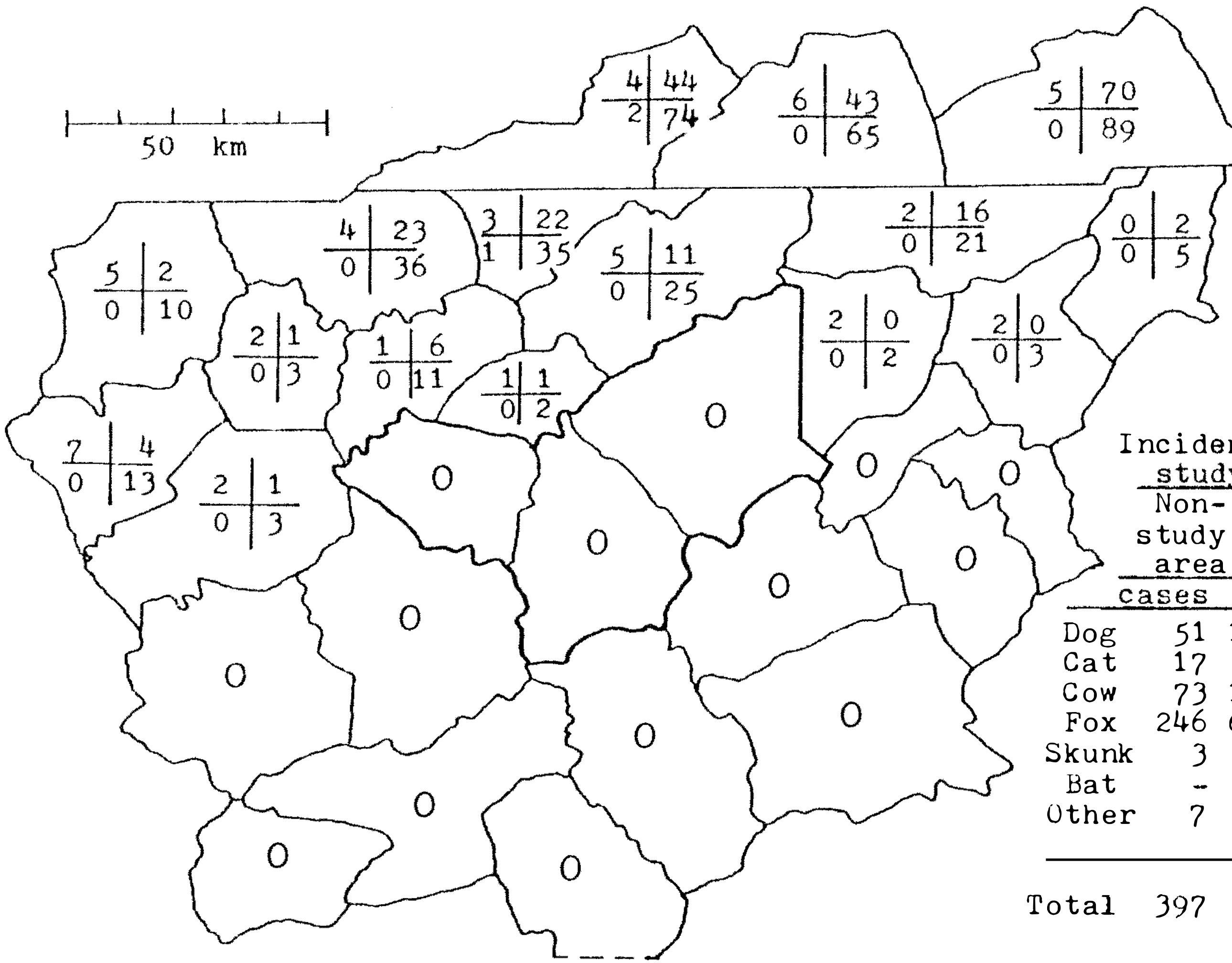
Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

O= no rabies cases

Incidence of rabies in the study region, 1954-1957

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	77	32	2	33	79	32
Cat	16	7	-		16	6
Cow	31	13	-		31	13
Fox	113	47	4	67	117	48
Skunk	-		-		-	
Bat	-		-		-	
Other	2	1	-		2	1
Total	239		6		245	

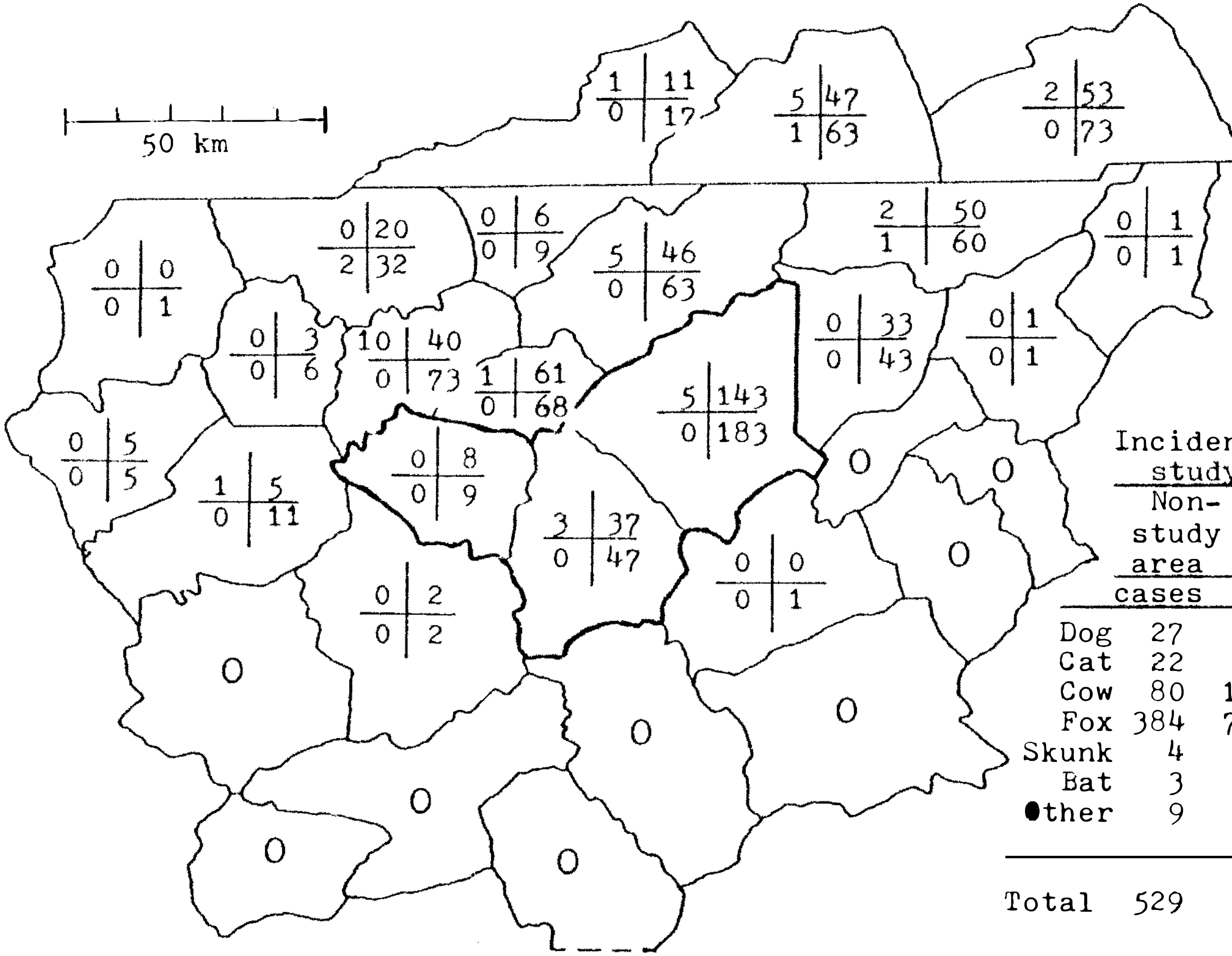
Fig. 42. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1954-1957. Three county study area shown in heavy outline.



Incidence of rabies in the study region, 1958-1961

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	51	13	-		51	13
Cat	17	4	-		17	4
Cow	73	18	-		73	18
Fox	246	62	-		246	62
Skunk	3	1	-		3	1
Bat	-		-		-	
Other	7	2	-		7	2
Total	397		0		397	

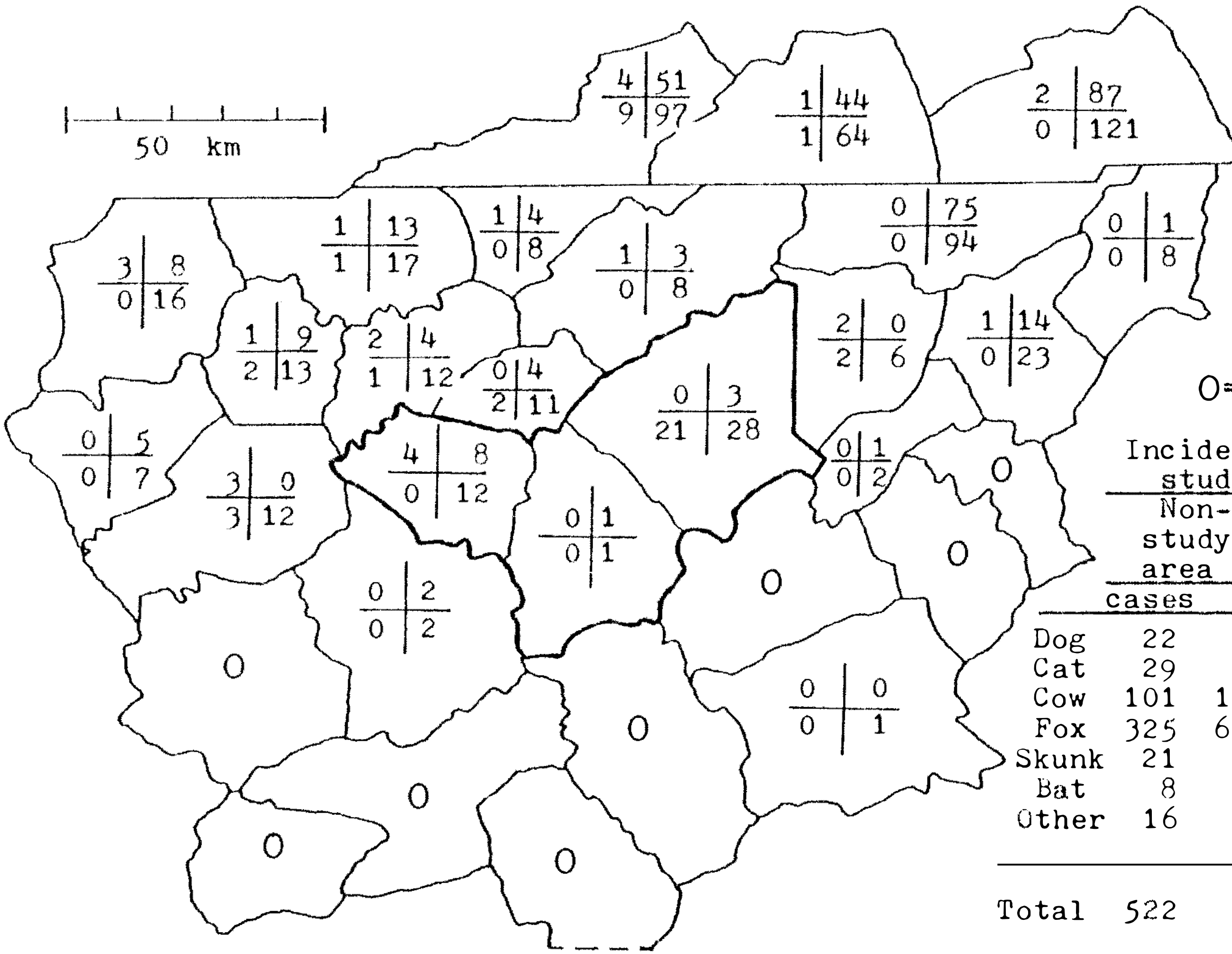
Fig. 43. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1958-1961. Three county study area shown in heavy outline.



Incidence of rabies in the study region, 1962-1965

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	27	5	8	3	35	5
Cat	22	4	7	3	29	4
Cow	80	15	33	14	113	15
Fox	384	73	188	79	572	74
Skunk	4	1	-		4	1
Bat	3	1	-		3	1
Other	9	2	3	1	12	2
Total	529		239		768	

Fig. 44. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1962-1965. Three county study area shown in heavy outline.



Key to map symbols

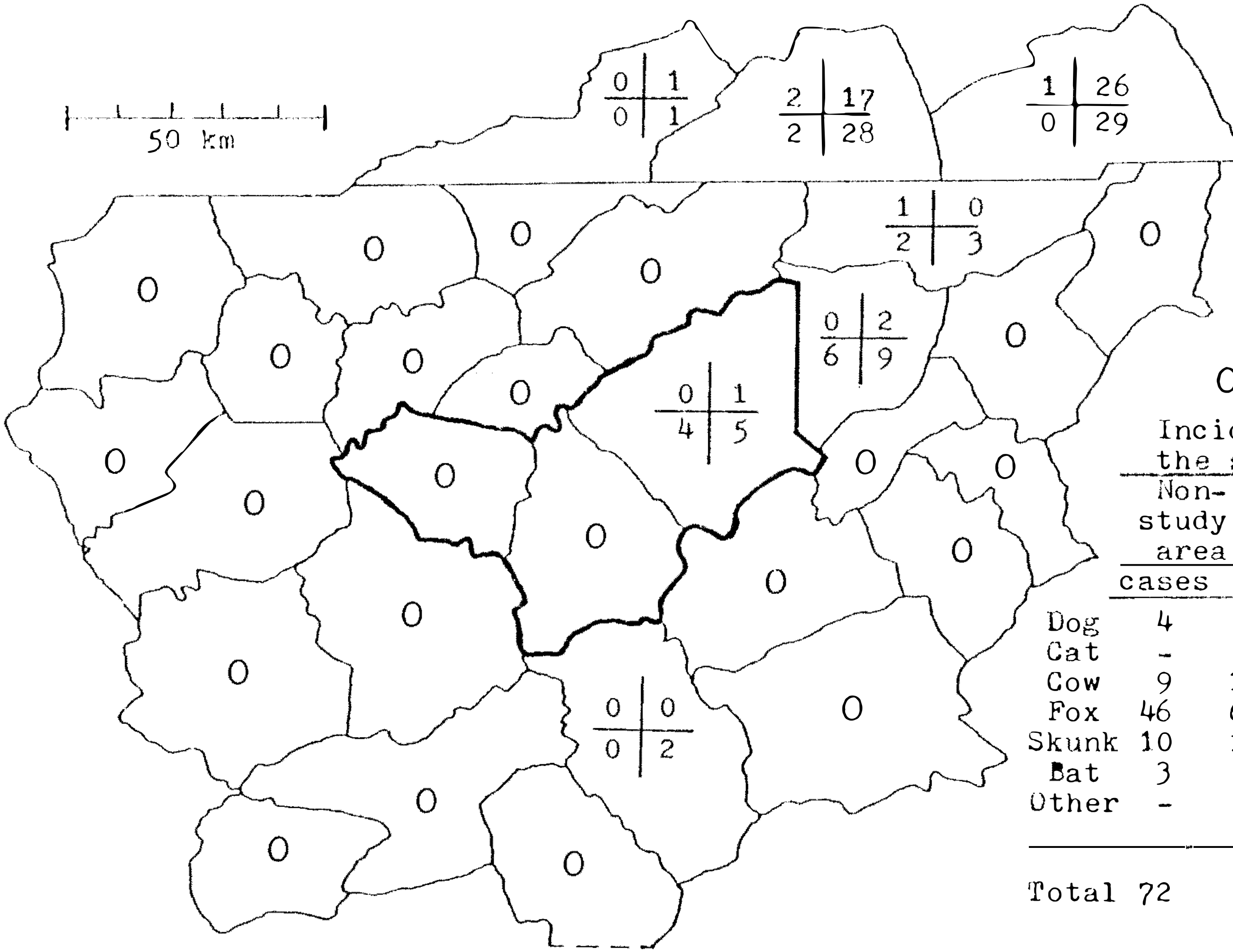
Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

O= no rabies cases

Incidence of rabies in the study region, 1966-1969

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	22	4	4	10	26	5
Cat	29	6	-		29	5
Cow	101	19	3	7	104	18
Fox	325	62	12	29	337	60
Skunk	21	4	21	51	42	7
Bat	8	2	-		8	1
Other	16	3	1	2	17	3
Total	522		41		563	

Fig. 45. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1966-1969. Three county study area shown in heavy outline.



Key to map symbols

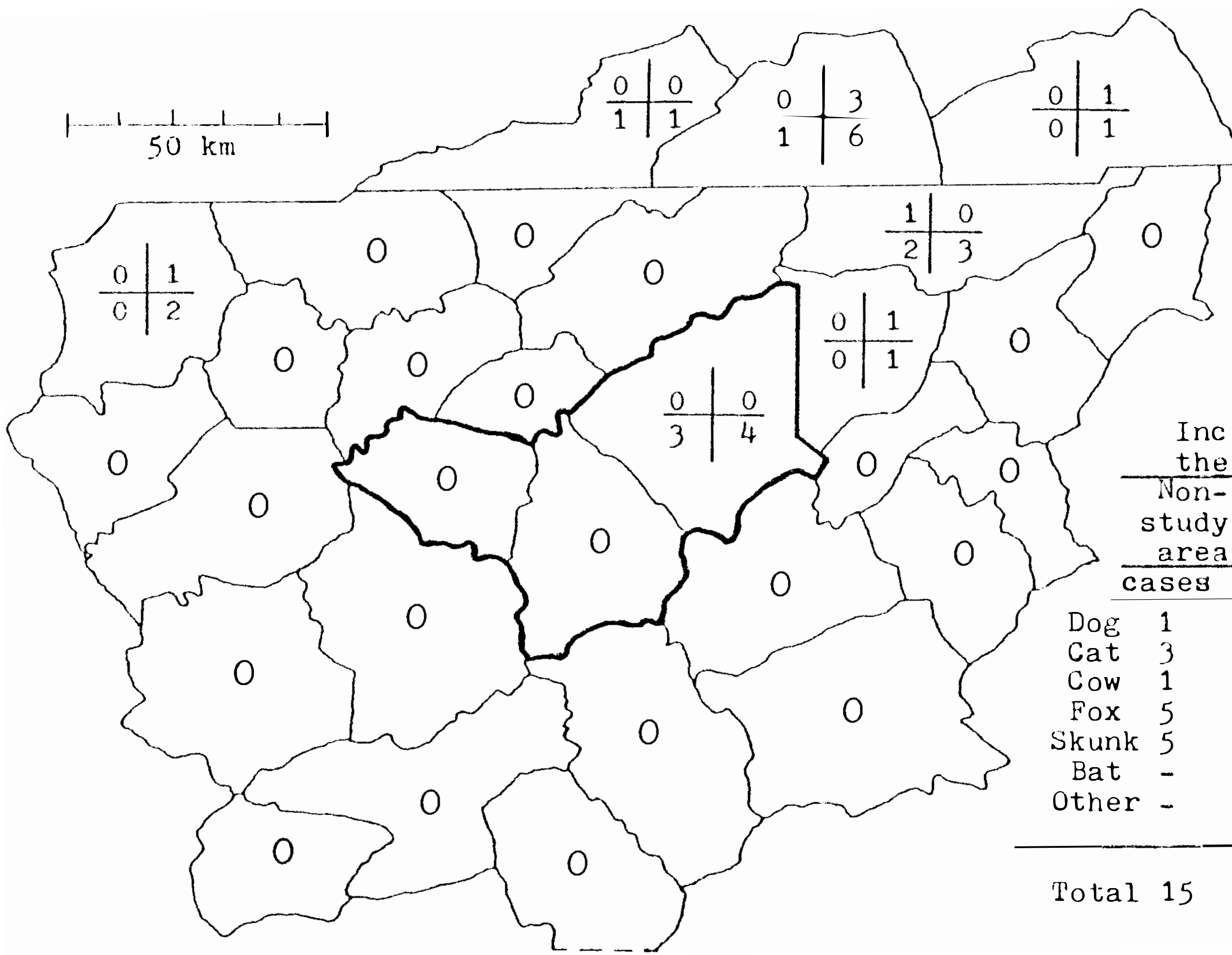
Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

O = no rabies cases

Incidence of rabies in the study region, 1970

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	4	6	-		4	5
Cat	-		-		-	
Cow	9	12	-		9	12
Fox	46	64	1	20	47	61
Skunk	10	14	4	80	14	18
Bat	3	4	-		3	4
Other	-		-		-	
Total	72		5		77	

Fig. 46. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1970. Three county study area shown in heavy outline.



Key to map symbols

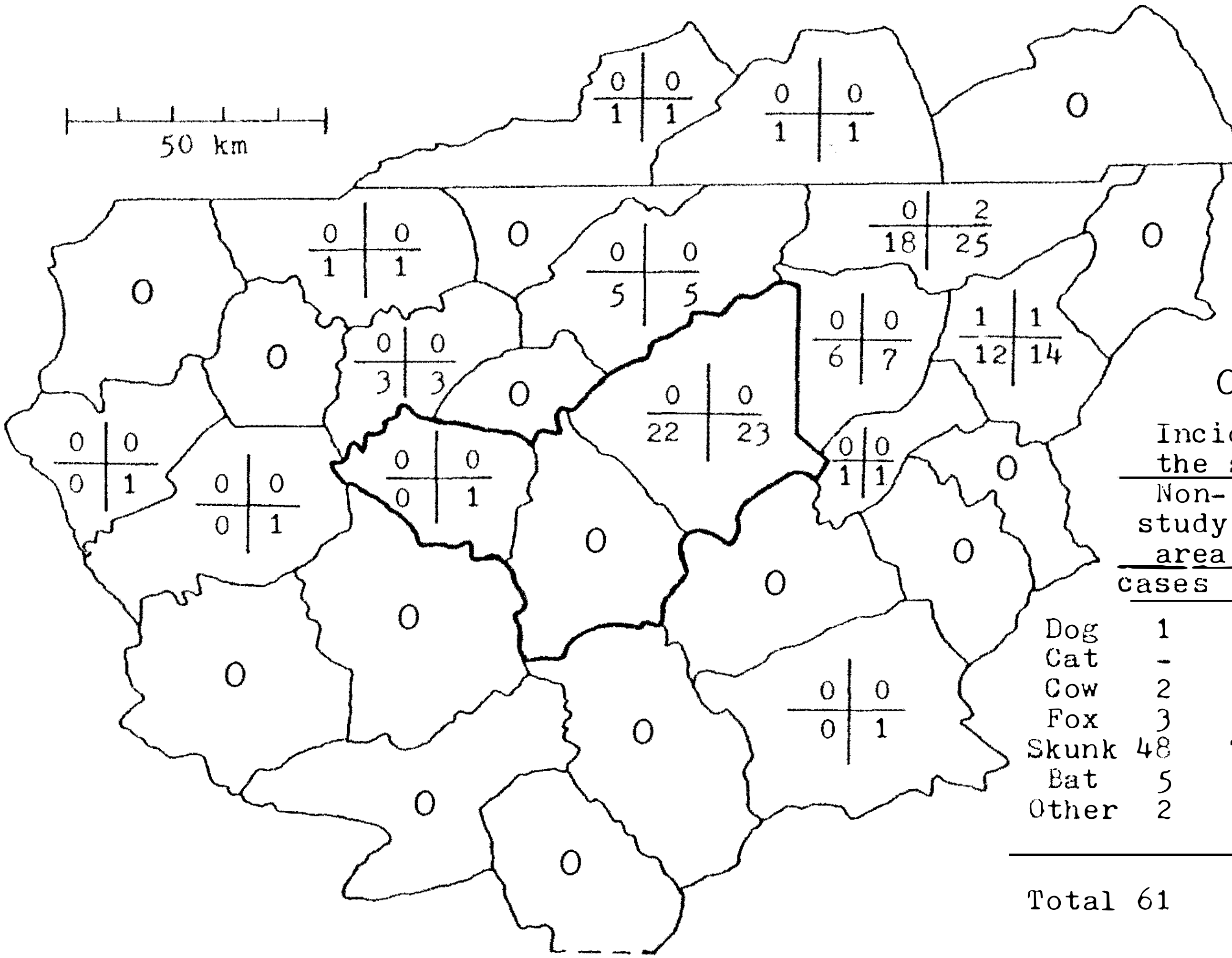
Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

O = no rabies cases

Incidence of rabies in the study region, 1971

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	1	7	-		1	5
Cat	3	20	-		3	16
Cow	1	7	-		1	5
Fox	5	33	-		5	26
Skunk	5	33	3	75	8	42
Bat	-		1	25	1	5
Other	-		-		-	
Total	15		4		19	

Fig. 47. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1971. Three county study area shown in heavy outline.



Key to map symbols

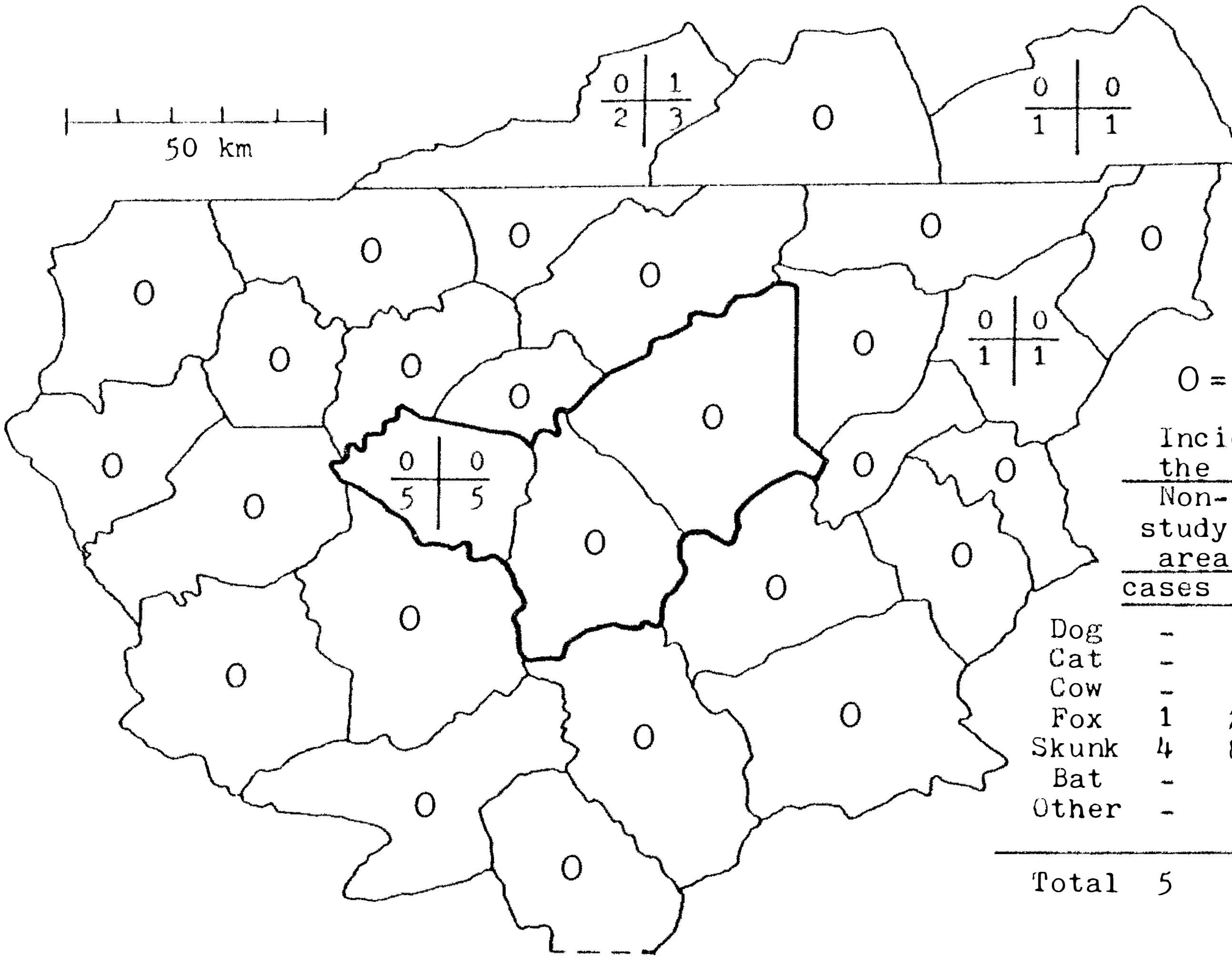
Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

O = no rabies cases

Incidence of rabies in the study region, 1972

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	1	2	-		1	1
Cat	-		-		-	
Cow	2	3	2	8	4	5
Fox	3	5	-		3	4
Skunk	48	79	22	92	70	82
Bat	5	8	-		5	6
Other	2	3	-		2	2
Total	61		24		85	

Fig. 48. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1972. Three county study area shown in heavy outline.



Key to map symbols

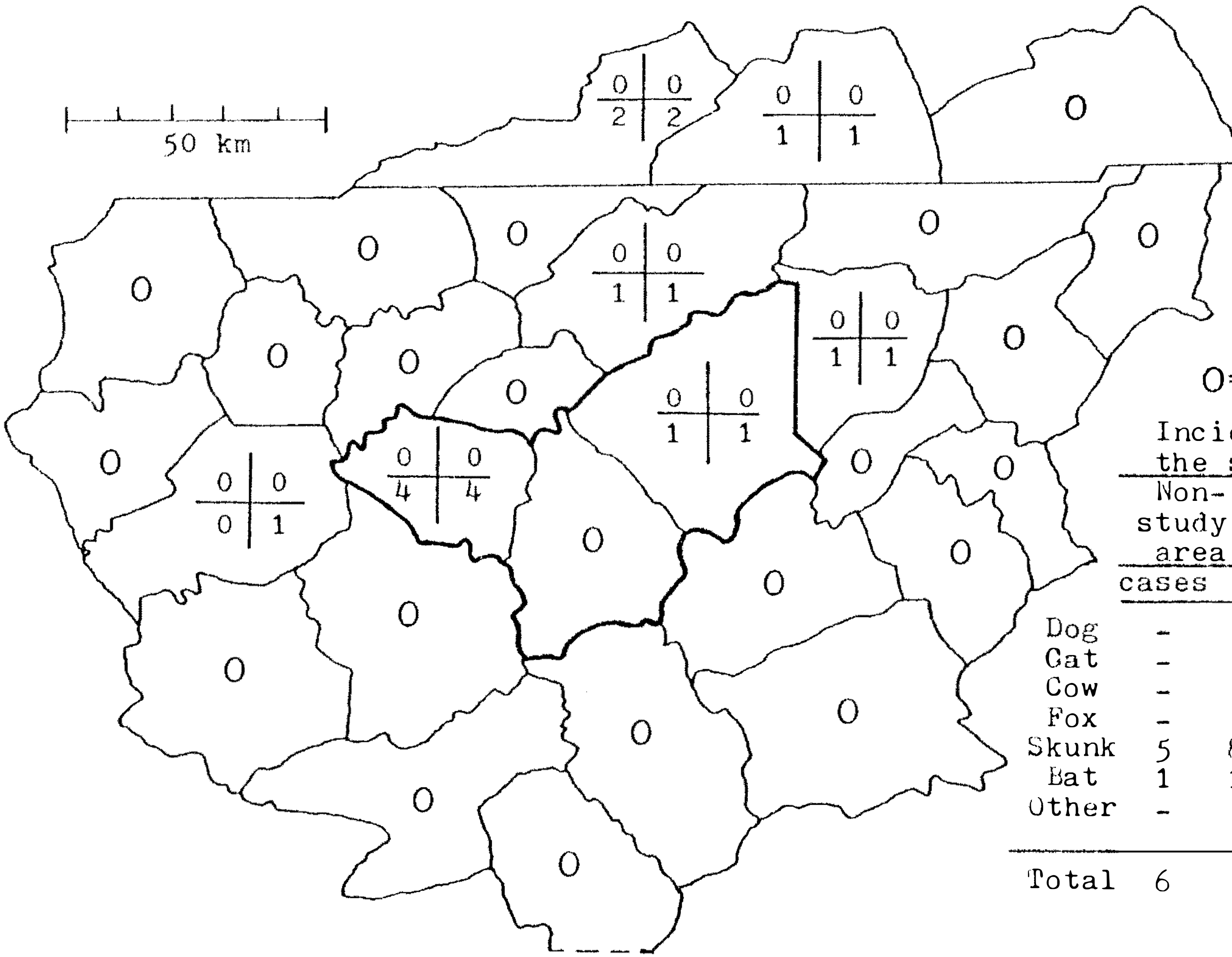
Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

O = no rabies cases

Incidence of rabies in the study region, 1973

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	-		-		-	
Cat	-		-		-	
Cow	-		-		-	
Fox	1	20	-		1	10
Skunk	4	80	5	100	9	90
Bat	-		-		-	
Other	-		-		-	
Total	5		5		10	

Fig. 49. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1973. Three county study area shown in heavy outline.



Key to map symbols

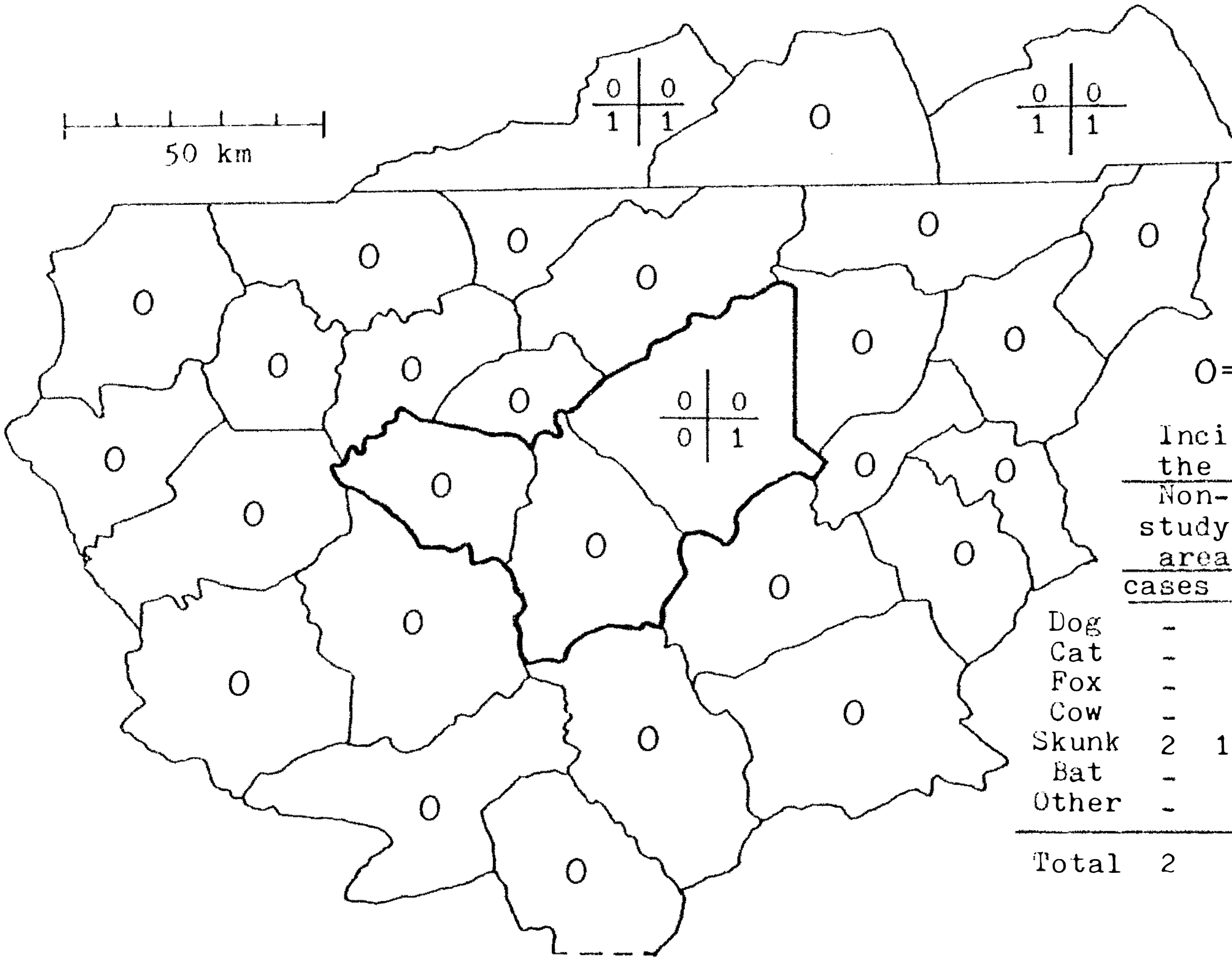
Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

O= no rabies cases

Incidence of rabies in the study region, 1974

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	-		-		-	
Cat	-		-		-	
Cow	-		-		-	
Fox	-		-		-	
Skunk	5	83	5	100	10	91
Bat	1	17	-		1	9
Other	-		-		-	
Total	6		5		11	

Fig. 50. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1974. Three county study area shown in heavy outline.



Key to map symbols

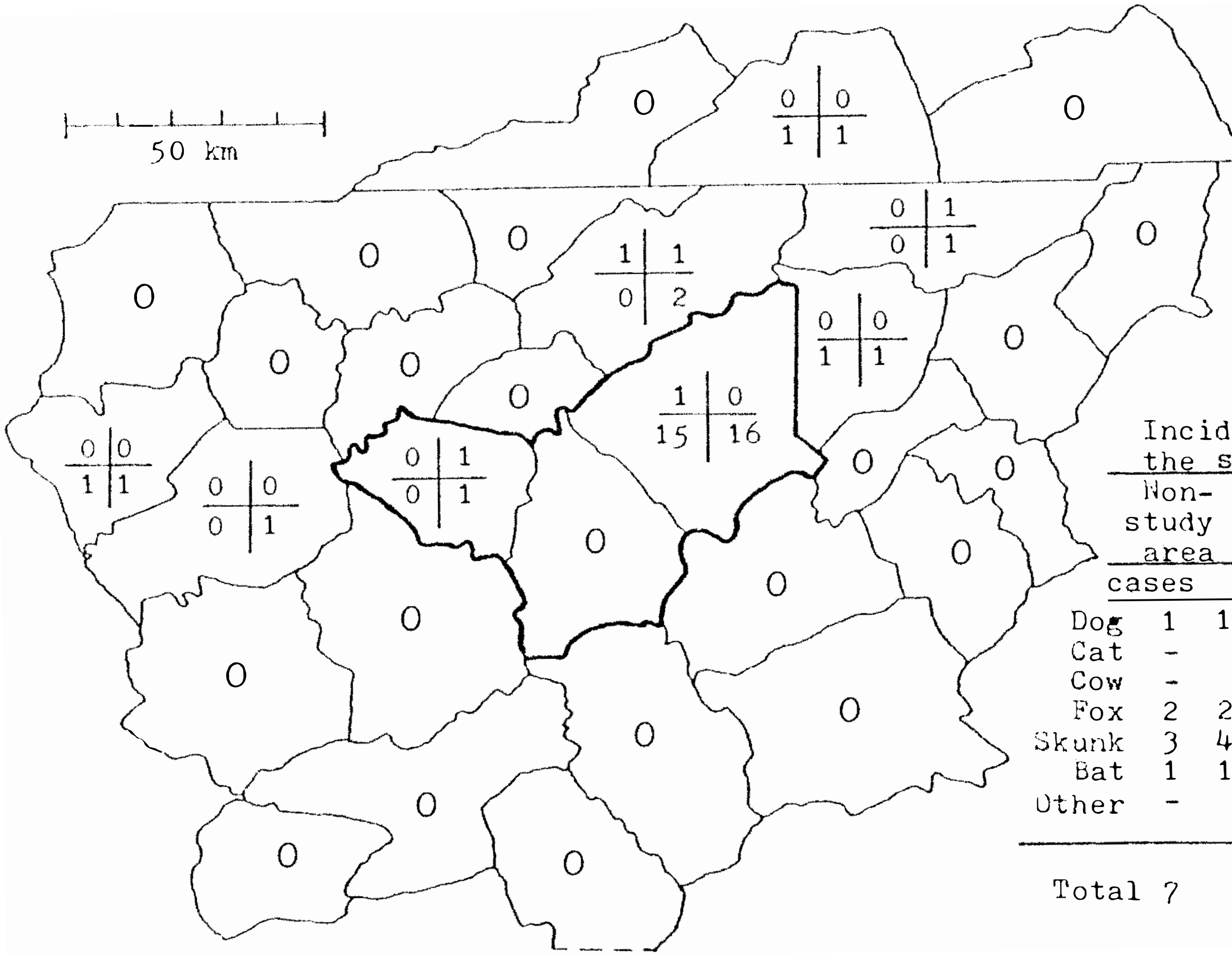
Dog rabies cases	Fox rabies cases
Skunk rabies cases	Total rabies cases

O = no rabies cases

Incidence of rabies in the study region, 1975

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	-		-		-	
Cat	-		-		-	
Fox	-		-		-	
Cow	-		-		-	
Skunk	2	100	-		2	67
Bat	-		-		-	
Other	-		1	100	1	33
Total	2		1		3	

Fig. 51. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1975. Three county study area shown in heavy outline.



Incidence of rabies in the study region, 1976

	Non-study area cases	%	Study area cases	%	Total cases	%
Dog	1	14	1	6	2	8
Cat	-		-		-	
Cow	-		-		-	
Fox	2	29	1	6	3	12
Skunk	3	43	15	88	18	75
Bat	1	14	-		1	4
Other	-		-		-	
Total	7		17		24	

Fig. 52. Incidence of laboratory confirmed rabies among the major animal categories in the 30 county study region, 1976. Three county study area shown in heavy outline.

APPENDIX H

RABIES HISTORY OF JEFFERSON, COCKE, AND GREENE COUNTIES, TENNESSEE, 1946-1976

Table 53. Rabies history of Jefferson County, Tennessee.[a]

Year	Dog	Cat	Cow	Fox	Skunk	Other	Total
1946	1/1*	0/ *	2/2*	0/ *	0/ *	0/ *	3/ 3*
1947	1/1*	0/ *	0/ *	0/ *	0/ *	0/ *	1/ 1*
1948	2/2*	1/ 1*	1/1*	0/ *	0/ *	0/ *	4/ 4*
1949	2/2*	1/ 1*	0/ *	0/ *	0/ *	0/ *	3/ 3*
1950	0/1	0/ 0	0/1	0/ 0	0/0	0/0	0/ 2
1951	0/1	0/ 0	0/0	0/ 1	0/0	0/0	0/ 2
1952	2/2*	0/ 1	0/0	0/ 0	0/0	0/0	2/ 3*
1953	0/1	0/ 0	0/0	0/ 0	0/0	0/0	0/ 1*
1954[b]	0/2	0/ 1	0/0	0/ 1	0/1	0/0	0/ 5
1955	0/0	0/ 1	0/0	0/ 1	0/0	0/0	0/ 2
1956	1/2	0/ 0	0/0	0/ 0	0/0	0/2	1/ 4
1957	0/2	0/ 0	0/0	0/ 0	0/0	0/0	0/ 2
1958	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ 7[c]
1959	0/1	0/ 1	0/0	0/ 0	0/0	0/1	0/ 3
1960	0/0	0/ 0	0/0	0/ 0	0/0	0/0	0/ 0
1961	0/0	0/ 0	0/0	0/ 0	0/0	0/2	0/ 2
1962	0/3	0/ 0	0/3	0/ 1	0/0	0/1	0/ 8
1963	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ 8[c]
1964	0/3	0/ 0	0/3	0/ 2	0/0	0/0	0/ 8
1965	0/8	0/14	1/3	8/30	0/0	0/4	9/59
1966	2/3	0/ 1	0/3	6/ 9	0/0	0/1	8/17
1967	2/3	0/ 2	0/3	2/ 6	0/0	0/2	4/16
1968	0/5	0/ 4	0/0	0/ 1	0/0	0/5	0/15
1969	0/2	0/ 8	0/0	0/ 0	0/0	0/1	0/11
1970	0/3	0/ 3	0/0	0/ 1	0/0	0/7	0/14
1971	0/5	0/ 2	0/0	0/ 0	0/0	0/4	0/11
1972	0/6	0/ 4	1/1	0/ 3	0/0	0/2	1/16
1973	0/5	0/ 7	0/0	0/ 1	5/5	0/2	5/20
1974	0/6	0/ 4	0/1	0/ 0	4/4	0/1	4/16
1975	0/5	0/ 7	0/1	0/ 0	0/0	0/0	0/13
1976	0/3	0/ 6	0/1	1/ 3	0/0	0/2	1/15
Total	13/78*	2/68*	5/23*	17/60*	9/10*	0/37*	46/291*

[a]Data show the number of confirmed rabies/cases/the number of animals examined, 1946-1976.

[b]State-wide rabies vaccination program initiated.

[c]Total based on annual state summary.

*Data not available or incomplete.

Table 54. Rabies history of Cocke County, Tennessee.[a]

Year	Dog	Cat	Cow	Fox	Skunk	Other	Total
1946	2/ 2*	0/ *	0/ *	0/ *	0/ *	0/ *	2/ 2*
1947	2/ 5	0/0	0/0	0/ 0	0/0	0/0	2/ 5*
1948	2/ 2*	0/3	3/4	1/ 1	0/0	0/0	6/10*
1949	1/ 2	0/0	0/0	0/ 1	0/0	0/1	1/ 4
1950	0/ 0	0/0	1/2	0/ 0	0/0	0/0	1/ 2
1951	0/ 0	0/0	0/0	0/ 0	0/0	0/0	0/ 0
1952	1/ 4	0/1	0/0	0/ 0	0/0	0/0	1/ 5
1953	0/ 1	0/0	0/0	0/ 0	0/0	0/0	0/ 1
1954[b]	1/ 3	0/1	0/0	4/ 4	0/0	0/1	5/ 9
1955	0/ 1	0/0	0/1	0/ 0	0/0	0/1	0/ 3
1956	0/ 2	0/2	0/0	0/ 0	0/0	0/0	0/ 4
1957	0/ 1	0/4	0/0	0/ 0	0/0	0/1	0/ 6
1958	0/ 3	0/1	0/0	0/ 0	0/0	0/0	0/ 4
1959	0/ 1	0/0	0/0	0/ 0	0/0	0/0	0/ 1
1960	0/ 1	0/0	0/0	0/ 0	0/0	0/1	0/ 2
1961	0/ 1	0/1	0/0	0/ 0	0/0	0/1	0/ 3
1962	0/ 1	0/2	0/0	0/ 0	0/0	0/0	0/ 3
1963	0/ 4	0/1	0/0	0/ 1	0/0	0/0	0/ 6
1964	0/10	0/2	2/4	28/34	0/0	0/2	31/52
1965	2/13	0/2	5/7	9/14	0/0	0/5	16/41
1966	0/ 4	0/3	0/5	0/ 0	0/0	0/7	0/19
1967	0/ 5	0/5	0/2	1/ 3	0/0	0/2	1/17
1968	0/ 4	0/1	0/0	0/ 0	0/0	0/0	0/ 5
1969	0/11	0/1	0/0	0/ 2	0/0	0/0	0/14
1970	0/ 7	0/5	0/0	0/ 1	0/0	0/1	0/14
1971	0/ 4	0/0	0/2	0/ 1	0/0	0/3	0/10
1972	0/ 9	0/4	0/3	0/ 2	0/0	0/7	0/25
1973	0/ 6	0/1	0/1	0/ 2	0/0	0/3	0/13
1974	0/ 6	0/6	0/1	0/ 4	0/0	0/5	0/22
1975	0/ 9	0/2	0/1	0/ 2	0/0	0/4	0/18
1976	0/ 6	0/2	0/0	0/ 2	0/0	0/1	0/11
Total	12/128*	0/50*	11/33*	43/74*	0/0	0/46*	66/331*

[a]Data show the number of confirmed rabies cases/the number of animals examined, 1946-1976.

[b]State-wide rabies vaccination program initiated.

*Data not available or incomplete.

Table 55. Rabies history of Greene County, Tennessee.[a]

Year	Dog	Cat	Cow	Fox	Skunk	Other	Total
1946	3/ 3*	1/ 1*	1/ 1*	0/ *	0/ *	0/ *	5/ 5*
1947	13/13*	0/ *	3/ 3*	1/ 1*	0/ *	0/ *	17/ 17*
1948	2/ 2*	2/ 2*	2/ 2*	2/ 2*	0/ *	0/ *	8/ 8*
1949	2/ 2*	1/ 1*	0/ *	0/ *	0/ *	0/ *	3/ 3*
1950	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *
1951	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *
1952	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *
1953	1/ 1*	0/ *	0/ *	0/ *	0/ *	0/ *	1/ 1*
1954[b]	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *
1955	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *
1956	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *
1957	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *
1958	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ 17[c]
1959	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *
1960	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ 12[c]
1961	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ 21[c]
1962	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ 18[c]
1963	0/ *	0/ *	0/ *	0/ *	0/ *	0/ *	0/ 18[c]
1964	4/33	4/38	12/21	101/137	0/ 0	0/21	121/250
1965	1/31	3/36	13/28	42/ 68	0/ 0	3/19	62/182
1966	0/13	0/13	1/ 4	0/ 4	0/ 2	0/ 8	1/ 44
1967	0/12	0/ 8	0/ 3	1/ 6	0/ 0	0/ 8	1/ 37
1968	0/11	0/ 8	0/ 0	0/ 2	0/ 2	0/12	0/ 35
1969	0/25	0/12	2/ 6	2/ 7	21/26	1/16	26/ 92
1970	0/13	0/11	0/ 3	1/ 13	4/ 4	0/ 7	5/ 51
1971	0/12	0/20	0/ 1	0/ 8	3/ 3	1/ 9	4/ 53
1972	0/18	0/27	1/ 2	0/ 21	22/25	0/16	23/109
1973	0/16	0/13	0/ 0	0/ 4	0/ 0	0/10	0/ 43
1974	0/ 5	0/14	0/ 0	0/ 11	1/ 1	0/ 7	1/ 38
1975	0/ 7	0/ 9	0/ 3	0/ 6	0/ 0	1/ 7	1/ 32
1976	1/16	0/15	0/ 1	0/ 7	15/19	0/17	16/ 75
Total	27/233*	11/228*	35/78*	150/297*	66/82*	6/157*	295/1,161*

[a]Data show the number of confirmed rabies cases/the number of animals examined, 1946-1976.

[b]State-wide rabies vaccination program initiated.

[c]Total based on annual state summary.

*Data not available or incomplete.

APPENDIX I

ANNUAL INCIDENCE OF REPORTED RABIES IN THE STUDY AREA, BY MONTH, BY ANIMAL CATEGORY, 1972-1976

Table 56. Incidence of reported rabies in the study area, 1972.[a]

Month	Jefferson County						Cocke County						Greene County						Total
	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	
Jan.	-	-	-	-	-	-	0/*	0/*	0/1	0/*	-	0/*	0/1	0/2	-	0/1	1/1	0/2	1/10
Feb.	-	0/1	-	-	-	-	0/2	-	-	-	-	-	-	0/2	-	0/2	2/2	-	2/ 9
Mar.	0/1	-	-	0/1	-	-	0/*	0/*	0/*	0/*	-	0/*	0/3	0/3	-	0/6	12/12	0/2	12/30
Apr.	-	-	-	-	-	-	0/*	0/*	0/*	0/*	-	0/*	0/2	0/2	0/1	0/4	3/5	0/2	3/19
May	0/2	-	-	-	-	-	-	-	-	-	-	-	0/*	0/3	-	0/2	2/*	0/*	2/13
June	-	-	-	-	-	0/1	0/*	0/*	0/*	0/*	-	0/*	0/2	0/5	-	-	1/1	0/2	1/14
July	0/1	0/2	-	-	-	-	-	0/1	-	-	-	0/1	0/*	0/1	-	0/3	1/*	0/*	1/14
Aug.	0/1	-	-	0/1	-	-	0/2	-	-	-	-	-	0/3	0/4	1/1	0/1	-	-	1/13
Sept.	-	-	1/1	-	-	-	-	-	-	-	-	0/1	0/2	0/2	-	-	0/*	0/*	1/ 8
Oct.	-	-	-	-	-	-	0/*	0/*	0/*	0/*	-	0/*	-	0/1	-	0/1	-	0/1	0/ 5
Nov.	-	-	-	-	-	0/1	0/*	0/*	0/*	0/*	-	0/*	0/*	0/1	-	0/1	-	0/2	0/ 9
Dec.	0/1	0/1	-	0/1	-	-	0/2	-	-	-	-	-	-	0/1	-	-	-	-	0/ 6
Group totals:																			
Dog	0/6						0/9						0/18						0/33
Cat		0/4						0/4						0/27					0/35
Cow			1/1						0/3						1/2				2/ 6
Fox				0/3						0/2						0/21			0/26
Skunk					-						-						22/25		22/25
Other						0/2						0/7						0/16	0/25
Total			1/16						0/25						23/109				24/150

[a]Data show number of rabid animals/total number examined. Sk = skunk, Oth = other animals.

*Exact data not available with totals based on annual summaries giving separate totals for month and species.

Table 57. Incidence of reported rabies in the study area, 1973.[a]

Month	Jefferson County						Cocke County						Greene County						Total
	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	
Jan.	-	0/1	-	-	-	-	0/1	-	-	-	-	-	0/1	-	-	-	-	0/1	0/ 4
Feb.	0/1	-	-	0/1	-	-	-	-	-	-	-	-	-	0/2	-	-	-	0/2	0/ 6
Mar.	0/1	-	-	-	3/3	-	0/1	-	-	0/1	-	-	0/2	-	-	0/2	-	-	3/10
April	-	-	-	-	1/1	-	-	-	-	-	-	-	-	-	-	-	-	0/1	1/ 2
May	0/1	0/1	-	-	-	-	0/1	-	0/1	0/1	-	0/3	0/2	0/1	-	-	-	-	0/11
June	-	-	-	-	-	-	-	-	-	-	-	-	-	0/2	-	0/1	-	-	0/ 3
July	-	0/1	-	-	-	0/1	0/1	-	-	-	-	-	0/4	0/1	-	0/1	-	-	0/ 9
Aug.	0/3	-	-	-	1/1	-	0/1	0/1	-	-	-	-	0/4	0/2	-	-	-	0/1	1/13
Sept.	0/1	-	-	-	-	-	-	-	-	-	-	-	0/1	-	-	-	-	0/1	0/ 3
Oct.	0/1	0/1	-	-	-	0/1	0/1	-	-	-	-	-	0/1	0/2	-	-	-	0/2	0/ 9
Nov.	-	-	-	-	-	-	-	-	-	-	-	-	-	0/1	-	-	-	0/1	0/ 2
Dec.	-	-	-	-	-	-	-	-	-	-	-	-	0/1	0/2	-	-	-	0/1	0/ 4
Group totals:																			
Dog	0/5						0/6						0/16						0/27
Cat		0/7						0/1						0/13					0/21
Cow			-						0/1						-				0/ 1
Fox				0/1						0/2						0/4			0/ 7
Skunk					5/5						-						-		5/ 5
Other						0/2						0/3						0/10	0/15
Total			5/20						0/13						0/43				5/76

[a]Data show number of rabid animals/total number examined. Sk = skunk, Oth = other animals.

Table 58. Incidence of reported rabies in the study area, 1974.[a]

Month	Jefferson County						Cocke County						Greene County						Total
	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	
Jan.	-	-	-	-	-	-	0/1	0/1	0/1	0/1	-	-	-	0/1	-	0/1	-	0/1	0/ 7
Feb.	-	-	-	-	-	-	-	-	-	-	-	-	0/1	-	-	-	-	-	0/ 1
Mar.	-	0/1	-	-	-	-	0/1	-	-	-	-	0/*	-	-	-	0/1	-	0/2	0/ 6
Apr.	0/1	-	-	-	1/1	-	0/2	0/1	-	-	-	-	0/1	-	-	-	-	-	1/ 6
May	0/1	-	-	-	1/1	-	0/1	-	-	-	-	-	0/1	0/3	-	0/4	1/1	-	2/12
June	0/2	-	0/1	-	2/2	0/1	-	-	-	-	-	0/1	-	0/2	-	0/1	-	0/1	2/11
July	-	0/1	-	-	-	-	0/*	0/1	-	0/1	-	0/*	0/1	-	-	-	-	0/2	0/ 7
Aug.	0/1	0/2	-	-	-	-	0/*	-	-	-	-	0/*	0/1	0/3	-	-	-	-	0/ 9
Sept.	-	-	-	-	-	-	-	0/1	-	0/1	-	0/1	-	0/1	-	-	-	-	0/ 4
Oct.	-	-	-	-	-	-	-	0/1	-	-	-	-	-	0/3	-	-	-	-	0/ 4
Nov.	-	-	-	-	-	-	-	-	-	-	-	0/1	-	-	-	-	-	-	0/ 1
Dec.	0/1	-	-	-	-	-	-	-	-	0/1	-	-	-	0/1	-	0/4	-	0/1	0/ 8
Group totals:																			
Dog	0/6						0/6						0/5						0/17
Cat		0/4						0/5						0/14					0/23
Cow			0/1						0/1						-				0/ 2
Fox				-						0/4						0/11			0/15
Skunk					4/4						-						1/1		5/ 5
Other						0/1						0/6						0/7	0/14
Total			4/16						0/22						1/38				5/76

[a]Data show number of rabid animals/total number examined. Sk = skunk, Oth = other animals.

*Exact data not available, with totals based on annual summaries giving separate totals for month and species.

Table 59. Incidence of reported rabies in the study area, 1975.[a]

Month	Jefferson County						Cocke County						Greene County						Total
	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	
Jan.	-	-	-	-	-	-	-	-	-	0/1	-	-	0/1	0/1	-	0/1	-	0/1	0/ 5
Feb.	0/1	-	-	-	-	-	0/1	-	-	-	-	0/1	-	-	-	-	-	-	0/ 3
Mar.	0/1	-	-	-	-	-	0/1	-	-	0/1	-	-	-	-	-	0/2	-	-	0/ 5
April	0/1	0/1	-	-	-	-	0/2	-	-	-	-	0/1	0/1	-	-	0/1	-	1/1	1/ 8
May	-	0/1	-	-	-	-	0/1	-	-	-	-	-	0/2	-	0/1	-	-	0/1	0/ 6
June	-	0/1	-	-	-	-	-	-	0/1	-	-	-	0/1	-	0/1	0/1	-	-	0/ 5
July	-	0/1	-	-	-	-	0/1	-	-	-	-	-	-	0/3	0/1	-	-	0/2	0/ 8
Aug.	0/2	-	-	-	-	-	0/2	-	-	-	-	-	0/1	0/1	-	-	-	0/1	0/ 7
Sept.	-	0/1	0/1	-	-	-	0/1	-	-	-	-	-	0/1	0/1	-	0/1	-	-	0/ 6
Oct.	-	0/1	-	-	-	-	-	-	-	-	-	0/1	-	0/1	-	-	-	-	0/ 3
Nov.	-	-	-	-	-	-	-	-	-	-	-	0/1	-	-	-	-	-	-	0/ 1
Dec.	-	0/1	-	-	-	-	-	0/2	-	-	-	-	-	0/2	-	-	-	0/1	0/ 6
Group totals:																			
Dog	0/5						0/9						0/7						0/21
Cat		0/7						0/2						0/9					0/18
Cow			0/1						0/1						0/3				0/ 5
Fox				-						0/2						0/6			0/ 8
Skunk					-						-						-		-
Other animals						-						0/4						1/7	1/11
Total			0/13						0/18						1/32				1/63

[a]Data show number of rabid animals/total number examined. Sk = skunk, Oth = other animals.

Table 60. Incidence of reported rabies in the study area, 1976.[a]

Month	Jefferson County						Cocke County						Greene County						Total
	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	Dog	Cat	Cow	Fox	Sk	Oth	
Jan.	-	0/1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0/ 1
Feb.	-	-	0/1	-	-	-	-	-	-	0/1	-	-	0/1	-	-	-	-	0/1	0/ 4
Mar.	-	-	-	0/1	-	-	0/2	-	-	-	-	-	0/1	-	-	-	3/3	-	3/ 8
Apr.	0/1	0/1	-	-	-	-	0/1	0/1	-	-	-	-	0/2	-	-	0/2	1/2	0/2	1/12
May	-	0/1	-	0/1	-	-	0/1	-	-	-	-	0/1	0/2	-	-	-	1/1	0/2	1/ 9
June	0/2	-	-	-	-	-	-	-	-	-	-	-	1/3	0/4	0/1	0/1	2/3	-	3/14
July	-	-	-	-	-	-	-	-	-	-	-	-	0/3	0/3	-	0/1	2/2	0/6	2/15
Aug.	-	0/1	-	-	-	0/1	0/1	0/1	-	-	-	-	-	0/3	-	-	1/1	0/2	1/10
Sept.	-	0/2	-	-	-	-	-	-	-	-	-	-	-	0/1	-	0/1	-	-	0/ 4
Oct.	-	-	-	-	-	-	0/1	-	-	0/1	-	-	-	0/2	-	-	1/1	0/1	1/ 6
Nov.	-	-	-	-	-	-	-	-	-	-	-	-	0/3	0/2	-	0/1	2/2	0/2	2/10
Dec.	-	-	-	1/1	-	-	-	-	-	-	-	-	0/1	-	-	-	2/4	0/1	3/ 8
Group totals:																			
Dog	0/3						0/6						1/16						1/25
Cat		0/6						0/2						0/15					0/23
Cow			0/1						-						0/1				0/ 2
Fox				1/3						0/2						0/7			1/12
Skunk					-						-						15/19		15/19
Other						0/2						0/1						0/17	0/20
Total			1/15						0/11						16/75				17/101

[a]Data show number of rabid animals/total number examined. Sk = skunk, Oth = other animals.

APPENDIX J

INCIDENCE OF REPORTED RABIES IN THE STUDY AREA WITH DATA COLLECTED IN INTERVIEWS WITH RESIDENTS SUBMITTING ANIMALS, 1972-1976

Table 61. Incidence of reported rabies in the study area with data collected in interviews with residents submitting the animals, 1972.

Case number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
72-1	3 Jan.	46 SE	Striped skunk	*	Adult	Morning	Barnyard	Movements sluggish, acting sick
72-2	3 Feb.	46 SE						
72-3	29 Feb.	40 NE	Striped skunk	*	Small adult	Noon	In yard near house	Movements very slow, no aggressive behavior
72-4	7 Mar.	39 NE	Striped skunk	*	Adult	Noon	In yard near house	Very little movement
72-5	7 Mar.	46 SE	Striped skunk	*	Adult	Morning	Dog pen near house	Found dead inside a wire enclosed dog pen, killed by dogs
72-6	10 Mar.	44 SE	Striped skunk	*	Adult	7:00 AM	Abandoned house, 80 m from home of resident	Movements incoordinated, disoriented
72-7	13 Mar.	*	*	*	*	*	*	*

Table 61. continued.

Case number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
72-8	13 Mar.	40 SW	Striped skunk	*	Adult	5:00 PM	Barn, 100 m from house	Movements slow, acting sick. No attempt to flee, no scenting
72-9	15 Mar.	42 SE	Striped skunk	*	Small adult	2:00 PM	In yard near house	Movements slow and sluggish
72-10	20 Mar.	39 SE	Striped skunk	*	*	Afternoon	Barn in pasture area	Acting sick, fighting with dogs
72-11	21 Mar.	34 SW	Striped skunk	*	Adult	7:30 PM	In barn 70 m from house	Found dead. Skunk had killed a chicken and carried it from hen house to barn
72-12	22 Mar.	46 NE	Striped skunk	*	Adult	10:00 AM	In pasture 100 m from house	Movements uncoordinated, moving in circles. No interaction with domestic animals. Condition good.
72-13	28 Mar.	44 SE	Striped skunk	*	*	*	*	*
72-14	28 Mar.	34 SW	Striped skunk	*	Adult	Midday	Edge of stream 40 m from house	No aggressive behavior

Table 61. continued.

Case number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
72-15	28 Mar.	39 NW	Striped skunk	*	Adult	Morning	In yard near house	Movements rapid, attacked by dogs
72-16	7 April	34 SW	Striped skunk	*	Small adult	11:00 AM	Barn	Found dead
72-17	13 April	*	Skunk	*	*	*	*	*
72-18	26 April	*	Skunk	*	*	*	*	*
72-19	9 May	*	Skunk	*	*	*	*	*
72-20	16 May	*	Skunk	*	*	*	*	*
72-21	14 June	39 SE	Striped skunk	*	Small adult	8:30 AM	In yard near house	Wandering aimlessly, movements very slow, no aggressive behavior
72-22	14 July	*	Skunk	*	*	*	*	*
72-23	16 Aug.	43 NE	Cow	*	*	*	*	*
72-24	13 Sept.	8 NE	Cow	*	*	*	*	Resident believed the source of infection was a skunk. A skunk had recently been killed when it came near the house during the daytime.

*Data not noticed or otherwise not available.

Table 62. Incidence of reported rabies in the study area with data collected in interviews with residents submitting the animals, 1973-1975.

Case Number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
1973								
73-1	3 Mar.	2 SE	Striped skunk	*	*	8:00 AM	Near house, in dog pen	Seemed sick, staggering gait, no scenting
73-2	11 Mar.	1 SW	Striped skunk	*	*	Noon	Farmyard, near calf barn	Movements slow and sluggish
73-3	11 Mar.	1 SW (same as 73-2)	Striped skunk	*	*	Noon	Farmyard, near grain barn	Same as 73-2
73-4	13 April	2 SE	Striped skunk	*	Adult	1:00 PM	In yard near house	Movements fast, but uncoordinated, seemed to be choking, walking in circles
73-5	30 Aug.	1 NW	Striped skunk	*	"Rather small" Juvenile?	Early evening	In yard near house	Chased by dogs, no scenting
1974								
74-1	1 April	1 NE	Striped skunk	*	*	7:00 PM	In yard near house	Fighting with dogs, aggressive behavior, attacking dogs

Table 62. continued.

Case number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
74-2	1 May	1 SE	Striped skunk	*	"About half grown"	Noon	In yard near house	Movements slow, came out from under house, appeared weak, no aggressive behavior
74-3	May	45 SE	Striped skunk	F	Adult	Afternoon	Barnyard near house	Behavior not observed, killed by dogs restricted to open kennel area
74-4	11 June	8 NW	Striped skunk	*	Adult	7:00 AM	On porch of house	Staggering gait, occasionally falling on side, no aggressive behavior
74-5	20 June	4 SW	Striped skunk	*	Adult	7:00 AM	In yard near house	Poor condition, patches of bare skin, movement sporadic, no response when approached by dogs
<u>1975</u>								
75-1	25 April	45 NE	Horse	*	*	*	*	No information on possible source of infection

*Data not noticed or otherwise not available.

Table 63. Incidence of reported rabies in the study area with data collected in interviews with residents submitting the animals, 1976.

Case number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
76-1	3 March	47 SW Farm V	Striped skunk	*	Small adult	8:00 AM	In yard near house	Moribund, unconscious, carried into yard by dogs
76-2	3 March	46 SE Farm GR	Striped skunk	*	*	Evening after dark	In yard near house	Moving about in yard, approached dogs restricted to kennel area
76-3	17 March	44 SE Farm B	Striped skunk	*	Small adult	Early morning	Farmyard near house	Fighting with dogs, attacked chickens, movements/gait appeared normal, condition poor, emaciated, and no scenting
76-4	14 April	40 SW Farm W	Striped skunk	*	Adult	Noon	In yard near house	Skunk fled when pursued by dogs, movements/gait appeared normal, did scent when attacked by dogs
76-5	4 May	44 SE Farm H	Striped skunk	*	Adult	Noon	In yard near house	Moving about in yard, some running, moved to dogs restricted to kennel area

Table 63. continued.

Case number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
76-6	7 June	44 NW Farm M	Striped skunk	Male	Adult	*	Open kennel area in woods 50 m from house	Found dead, killed by dogs restricted to open kennel area
76-7	9 June	44 SW	Striped skunk	*	Adult	1:00 PM	In yard near house	Very poor condition, mange, emaciated; movements slow, but ran directly toward resident before being shot
76-8	24 June	35 NW Farm F	Dog	*	*	*	*	Dog had recently fought with a striped skunk. Skunk had wandered into yard near house during afternoon. Skunk emaciated.
76-9	29 June (Report July)	47 NE Farm GO	Striped skunk	*	Small adult	5:00 PM	In yard near house	Behavior not observed skunk pursued by dogs
76-10	27 July	40 NW	Striped skunk	*	*	Evening, after dark	In yard near house	Movements slow, turning in circled. Detected, but not attacked by family dog.

Table 63. continued.

Case number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
76-11	27 Aug.	43 NE	Striped skunk	*	Adult	11:00 AM	In yard near house	Wandering about aimlessly, no aggressive behavior. Good condition. Appeared to be well fed, gait normal.
76-12	20 Oct.	43 NE	Striped skunk	*	Adult	4:30 PM	In yard near house	Walking in circles, disoriented, no aggressive behavior. Good condition, appeared well fed.
76-13	10 Nov.	46 SW	Striped skunk	*	Adult	Morning	In yard near house	Movements rapid, but incoordinated, falling over, staggering. Came directly toward resident before being shot. Good condition, not emaciated.
76-14	23 Nov.	34 SW	Striped skunk	*	Adult	Afternoon	Under house	Skunk was under house when attacked by dogs. Attempted to flee, but was killed by dogs.
76-15	23 Nov. (Report in Dec.)	3 NW	Gray fox	*	Adult	10:00 AM	Small woodlot near cropland	Fighting with dogs, appeared to be trying to flee, movements incoordinated. Condition good, not emaciated.

Table 63. continued.

Case number	Date	Location (trap area, quadrant)	Species	Sex	Age class	Time first seen	Type of site	Behavioral notes and other comments
76-16	1 Dec.	43 NE	Striped skunk	*	Adult	9:00 AM	In yard near house	Movements slow and sluggish
76-17	8 Dec.	43 NE	Striped skunk	*	Adult	Morning	In yard near house	Found dead. Appeared to be in good condition prior to death, not emaciated

*Data not noticed or otherwise not available.

APPENDIX K

RELATIVE ABUNDANCE AND DISTRIBUTION OF OPOSSUMS IN THE 48 TRAP AREAS AND SELECTED FARMS, 1973-1976

Table 64. Relative abundance and distribution of opossums in the 48 trap areas as expressed by capture rate, opossum captures per 100 trap nights (TN), and percentage of sites used which yielded one or more opossums, 1973.

Trap area	Number of		Capture	Trap sites			Trap area	Number of		Capture	Trap sites		
		Opossums			With capture(s)				Opossums			With capture(s)	
TA	TN	captured	rate	Used	Number	%	TA	TN	captured	rate	Used	Number	%
1	34	4	11.8	12	3	25.0	25	71	5	7.0	26	5	19.2
2	72	3	4.2	24	3	12.5	26	36	2	5.6	12	2	16.7
3	72	6	8.3	24	5	20.8	27	72	6	8.3	24	3	12.5
4	36	1	2.8	12	1	8.3	28	24	2	8.3	12	2	16.7
5	72	9	12.5	27	7	25.9	29	36	2	5.6	14	2	14.3
6	36	1	2.8	12	1	8.3	30	36	2	5.6	12	2	16.7
7	36	3	8.3	13	3	23.1	31	36	7	19.4	12	7	58.3
8	72	5	6.9	24	5	20.8	32	35	4	11.4	12	4	33.3
9	35	0	0	12	0	0	33	35	2	5.7	13	2	15.4
10	36	3	8.3	12	3	25.0	34	73	9	12.3	26	8	30.8
11	71	4	5.6	24	4	16.7	35	75	11	14.7	27	11	40.7
12	36	1	2.8	12	1	8.3	36	35	5	14.3	13	5	38.5
13	70	2	2.8	24	2	8.3	37	33	2	6.1	13	2	15.4
14	36	5	13.9	12	4	33.3	38	22	2	9.1	11	2	18.2
15	24	3	12.5	12	3	25.0	39	36	2	5.6	13	1	7.7
16	36	2	5.6	12	2	16.7	40	36	1	2.8	12	1	8.3
17	36	1	2.8	12	1	8.3	41	36	3	8.3	12	2	16.7
18	24	3	12.5	12	3	25.0	42	36	4	11.1	12	3	25.0
19	36	1	2.8	12	1	8.3	43	69	4	5.8	26	4	15.4
20	48	1	2.1	16	1	6.2	44	36	3	8.3	12	3	25.0
21	35	2	5.7	14	2	14.3	45	71	6	8.4	25	6	24.0
22	72	6	8.3	26	6	23.1	46	71	5	7.0	25	5	20.0
23	36	3	8.3	12	3	25.0	47	34	2	5.9	12	1	8.3
24	60	4	6.7	22	4	18.2	48	70	6	8.6	24	6	25.0
Subtotal	1,121	73	6.5	394	68	17.2		1,114	97	8.7	400	89	22.2
Study area total (TA 1-48)								2,235	170	7.5	794	157	19.8

Table 65. Relative abundance and distribution of opossums in the 48 trap areas as expressed by capture rate, opossum captures per 100 trap nights (TN), and percentage of sites used which yielded one or more opossums, 1974.

Trap area	Number of		Capture rate	Trap sites			Trap area	Number of		Capture rate	Trap sites		
					With capture(s)							With capture(s)	
TA	TN	Opossums captured		Used	Number	%	TA	TN	Opossums captured		Used	Number	%
1	88	13	14.8	25	9	36.0	25	36	1	2.8	12	1	8.3
Fm C	48	8	16.7	16	7	43.8	26	35	4	11.4	14	2	14.3
Fm K	48	5	10.4	18	5	27.8	27	38	4	10.5	13	4	30.8
2	36	3	8.3	12	3	25.0	28	37	5	13.5	13	5	38.5
3	36	3	8.3	13	3	23.1	29	66	6	9.1	18	5	27.8
4	73	8	11.0	23	5	21.7	30	39	2	5.1	13	2	15.4
5	36	5	13.9	12	5	41.7	31	68	7	10.3	21	6	28.6
6	75	4	5.3	24	4	16.7	32	36	6	16.7	13	6	46.2
7	36	4	11.1	12	3	25.0	33	64	4	6.2	21	4	19.0
8	35	3	8.6	12	3	25.0	34	38	2	5.3	12	2	16.7
9	36	5	13.9	12	4	33.3	35	33	3	9.1	11	3	27.3
10	38	7	18.4	13	7	53.8	36	37	1	2.7	14	1	7.1
11	36	8	22.2	12	6	50.0	37	37	2	5.4	13	2	15.4
12	63	3	4.8	22	2	9.1	38	34	3	8.8	13	3	23.1
13	36	2	5.6	13	2	15.4	39	37	2	5.4	13	2	15.4
14	32	2	6.2	12	2	16.7	40	72	6	8.3	23	5	21.7
15	36	2	5.6	13	1	7.7	41	32	2	6.2	14	2	14.3
16	35	2	5.7	12	2	16.7	42	35	3	8.6	12	3	25.0
17	36	3	8.3	12	2	16.7	43	34	2	5.9	12	2	16.7
18	38	3	7.9	13	3	23.1	44	65	7	10.8	22	6	27.3
19	34	6	17.6	14	4	28.6	45	38	6	15.8	13	5	38.5
20	68	3	4.4	24	2	8.3	46	33	2	6.1	13	2	15.4
21	36	0	0	13	0	0	47	36	0	0	13	0	0
22	36	2	5.6	16	2	12.5	48	35	7	20.0	13	7	53.8
23	36	3	8.3	13	3	23.1	Sub-total	1,015	87	8.3	349	80	22.9
24	39	1	2.6	14	1	7.1							
Sub-total	1,146	108	9.4	395	90	22.8	Total	2,161	195	9.0	744	170	22.8

Table 66. Relative abundance and distribution of opossums in the 48 trap areas as expressed by capture rate, opossum captures per 100 trap nights (TN), and percentage of sites used which yielded one or more opossums, 1975.

Trap area	Number of		Cap-ture	Trap sites			Trap area	Number of		Cap-ture	Trap sites		
		Opossums			With capture(s)				Opossums			With capture(s)	
TA	TN	captured	rate	Used	Number	%	TA	TN	captured	rate	Used	Number	%
1	37	7	18.9	13	6	46.2	25	37	2	5.4	14	2	14.3
2	33	2	6.1	11	2	18.2	26	32	1	3.1	12	1	8.3
3	42	5	11.9	15	4	26.7	27	35	9	25.7	15	6	40.0
4	34	7	20.6	13	5	38.5	28	31	7	22.6	11	6	54.5
5	31	8	25.8	12	7	58.3	29	35	10	28.6	13	9	69.2
6	38	6	15.8	14	5	35.7	30	35	8	22.8	13	7	53.8
7	36	9	25.0	14	8	57.1	31	39	9	23.1	13	7	53.8
8	36	6	16.7	13	5	38.5	32	34	9	26.5	12	8	66.7
9	35	12	34.3	13	8	61.5	33	33	5	15.2	13	4	30.7
10	39	7	17.9	14	7	50.0	34	30	2	6.7	12	2	16.7
11	37	3	8.1	13	3	23.1	35	35	6	17.1	13	5	38.7
12	35	8	22.8	12	6	50.0	36	33	7	21.2	13	7	53.8
13	35	6	17.1	12	6	50.0	37	43	10	23.2	15	8	53.3
14	36	8	22.2	12	6	50.0	38	36	7	19.4	12	6	50.0
15	36	10	27.8	12	8	66.7	39	31	8	25.8	11	6	54.5
16	34	8	23.5	12	8	66.7	40	35	7	20.0	13	4	30.8
17	35	5	14.3	12	5	41.7	41	33	4	12.1	14	4	28.6
18	30	5	16.7	11	5	45.4	42	35	10	28.6	16	8	50.0
19	30	6	20.0	13	5	38.5	43	39	5	12.8	13	4	30.8
20	40	8	20.0	14	7	50.0	44	37	4	10.8	13	4	30.8
21	33	7	21.2	15	7	46.7	45	38	4	10.5	13	3	23.1
22	35	9	25.7	15	6	40.0	46	32	9	28.1	12	7	58.3
23	35	3	8.6	14	3	21.4	47	33	9	27.3	14	8	57.1
24	40	2	5.0	14	2	14.3	48	35	5	14.3	13	4	30.8
Subtotal	852	157	18.4	313	134	42.8		836	157	18.8	313	130	41.5
			Study area total (TA 1-48)					1,688	314	18.6	626	264	42.2

Table 67. Relative abundance and distribution of opossums in trap areas and farms as expressed by capture rate, opossum captures per 100 trap nights (TN) and percentage of sites used which yielded one or more opossums, 1976.

Trap area TA	Number of TN	Number of Opossums captured	Capture rate	Trap sites Used	Trap sites With capture(s) Number	Trap sites With capture(s) %
1	27	12	44.4	9	7	77.8
2	15	3	20.0	5	2	40.0
10	28	8	28.6	10	7	70.0
11	18	8	44.4	6	5	83.3
16	15	5	33.3	5	3	60.0
Subtotal	103	36	34.9	35	24	68.6
34	3	0	0	1	0	0
35	32	10	31.2	11	8	72.7
Farm F	39	10	25.6	14	6	42.8
39	9	5	55.6	3	3	100.0
40	25	7	28.0	9	5	55.5
Farm W	34	4	11.8	12	3	25.0
43	9	5	55.6	3	1	33.3
44	35	9	25.7	13	8	61.5
Farm B	18	2	11.1	6	2	33.3
Farm H	39	2	5.1	14	2	14.3
Farm M	22	2	9.1	9	2	22.2
45	27	1	3.1	9	1	11.1
46	26	5	18.5	11	4	36.4
Farm GR	26	2	7.7	10	2	20.0
47	29	3	10.3	10	3	30.0
Farm GO	22	3	13.6	8	3	37.5
Farm V	23	1	4.3	9	1	11.1
48	27	7	25.9	8	5	62.5
Sub-total	445	78	17.5	160	59	36.9
Total	548	114	20.8	195	83	42.6

APPENDIX L

RELATIVE ABUNDANCE AND DISTRIBUTION OF CATS IN THE 48 TRAP AREAS AND SELECTED FARMS, 1973-1976

Table 68. Relative abundance and distribution of cats in the 48 trap areas as expressed by capture rate, cat captures per 100 trap nights, and the percentage of sites used which yielded one or more cats, 1973.[a]

Trap area	Cats captured	Capture rate	Trap sites with capture(s)		Trap area	Cats captured	Capture rate	Trap sites with capture(s)	
			Number	% of sites used				Number	% of sites used
1	2	5.9	1	8.3	25	0	0	0	0
2	5	6.9	1	16.7	26	2	5.6	2	16.7
3	1	1.4	1	4.2	27	5	6.9	5	20.8
4	0	0	0	0	28	2	8.3	2	16.7
5	3	4.2	3	11.1	29	2	5.6	1	7.1
6	3	8.3	3	25.0	30	3	8.3	3	25.0
7	2	5.6	2	15.4	31	3	8.3	2	16.7
8	6	8.3	6	25.0	32	3	8.6	2	16.7
9	2	5.7	2	16.7	33	4	11.4	4	30.8
10	1	2.8	1	8.3	34	6	8.2	6	23.1
11	4	5.6	4	16.7	35	2	2.7	2	7.4
12	5	13.9	5	41.7	36	2	5.7	2	15.4
13	4	5.7	4	16.7	37	4	12.1	4	30.8
14	2	5.6	2	16.7	38	0	0	0	0
15	0	0	0	0	39	3	8.3	3	23.1
16	2	5.6	2	16.7	40	2	5.6	2	16.7
17	5	13.9	5	41.7	41	1	2.8	1	8.3
18	1	4.2	1	8.3	42	4	11.1	4	33.3
19	2	5.6	2	16.7	43	8	11.6	8	30.8
20	1	2.1	1	6.2	44	2	5.6	2	16.7
21	1	2.8	1	7.1	45	8	11.3	8	32.0
22	2	2.8	2	7.7	46	3	4.2	3	12.0
23	0	0	0	0	47	2	5.9	2	16.7
24	0	0	0	0	48	5	7.1	5	20.8
Subtotal	54	4.8	52	13.2		76	6.8	70	17.5
			Study area total			130	5.8	122	15.4

[a]Numbers of trap nights and sites used are given in Table 41, page 419.

Table 69. Relative abundance and distribution of cats in the 48 trap areas as expressed by capture rate, cat captures per 100 trap nights, and the percentage of sites used which yielded one or more cats, 1974.[a]

Trap area	Cats captured	Capture rate	Trap sites with capture(s): Number	Trap sites with capture(s): % of sites used	Trap area	Cats captured	Capture rate	Trap sites with capture(s): Number	Trap sites with capture(s): % of sites used
1	5	9.1	5	20.0	25	0	0	0	0
Fm C	2	4.2	1	6.2	26	1	2.8	1	7.1
Fm K	5	10.4	3	16.7	27	1	2.8	1	7.7
2	1	2.8	1	8.3	28	1	2.6	1	7.7
3	4	11.1	4	30.8	29	0	0	0	0
4	0	0	0	0	30	4	10.2	3	23.1
5	0	0	0	0	31	1	1.5	1	4.8
6	2	2.7	2	8.3	32	3	8.3	3	23.1
7	1	2.8	1	8.3	33	2	3.1	2	9.5
8	5	14.3	5	41.7	34	1	2.6	1	8.3
9	2	5.6	2	16.7	35	1	3.0	1	9.1
10	2	5.3	2	15.4	36	1	2.8	1	7.1
11	1	2.8	1	8.3	37	4	10.8	3	23.1
12	6	9.5	5	22.7	38	1	2.9	1	7.7
13	0	0	0	0	39	3	8.1	3	23.1
14	1	3.1	1	8.3	40	5	6.9	4	17.4
15	0	0	0	0	41	1	3.1	1	7.1
16	1	2.8	1	8.3	42	4	11.4	4	33.3
17	3	8.3	3	25.0	43	3	8.8	3	25.0
18	1	2.6	1	7.7	44	4	6.2	4	18.2
19	2	5.6	2	14.3	45	1	2.6	1	7.7
20	2	2.9	2	8.3	46	3	9.1	2	15.4
21	2	5.6	2	15.4	47	0	0	0	0
22	3	8.3	3	18.8	48	1	2.8	1	7.7
23	0	0	0	0					
24	1	2.6	1	7.1					
Subtotal	52	4.5	48	12.2		46	4.0	42	12.0
			Study area total			98	4.5	90	12.1

[a]Numbers of trap nights and sites used are given in Table 42, page 420.

Table 70. Relative abundance and distribution of cats in the 48 trap areas as expressed by capture rate, cat captures per 100 trap nights, and the percentage of sites used which yielded one or more cats, 1975.[a]

Trap area	Cats captured	Capture rate	Trap sites with capture(s) Number	Trap sites with capture(s) % of sites used	Trap area	Cats captured	Capture rate	Trap sites with capture(s) Number	Trap sites with capture(s) % of sites used
1	1	2.7	1	7.7	25	3	8.1	3	21.4
2	1	3.0	1	9.1	26	1	3.1	1	8.3
3	5	11.9	3	20.0	27	3	8.6	3	20.0
4	2	5.9	2	15.4	28	3	9.7	3	27.3
5	1	3.2	1	8.3	29	3	8.6	3	23.1
6	0	0	0	0	30	0	0	0	0
7	3	8.3	3	21.4	31	1	2.6	1	7.7
8	4	11.1	3	23.1	32	4	11.8	4	33.3
9	3	8.6	3	23.1	33	3	9.1	3	23.1
10	2	5.1	2	14.3	34	4	13.3	3	25.0
11	1	2.7	1	7.7	35	4	11.4	3	23.1
12	2	5.7	2	16.7	36	0	0	0	0
13	5	14.3	5	41.7	37	1	2.3	1	6.7
14	1	2.8	1	8.3	38	6	16.7	6	50.0
15	2	5.6	2	16.7	39	2	6.4	2	18.2
16	3	8.8	3	25.0	40	5	14.3	5	38.5
17	5	14.3	3	25.0	41	3	9.1	3	21.4
18	4	13.3	4	36.4	42	1	2.8	1	6.2
19	2	6.7	2	15.4	43	3	7.7	3	23.1
20	2	5.0	2	14.3	44	4	10.8	4	30.8
21	1	3.0	1	6.7	45	4	10.5	3	23.1
22	0	0	0	0	46	1	3.1	1	8.3
23	3	8.6	3	21.4	47	1	3.0	1	7.1
24	1	2.5	1	7.1	48	3	8.6	3	23.1
Subtotal	54	6.3	49	15.6		63	7.5	60	19.2
			Study area total			117	6.9	109	17.4

[a]Numbers of trap nights and sites used are given in Table 43, page 421.

Table 71. Relative abundance and distribution of cats in the study area as expressed by capture rate, cat captures per 100 trap nights, and the percentage of sites used which yielded one or more cats, 1976.[a]

			Trap sites with capture(s)					Trap sites with capture(s)	
Trap area	Cats captured	Capture rate	Number	% of sites used	Trap area	Cats captured	Capture rate	Number	% of sites used
1	1	3.7	1	11.1	34	1	33.3	1	100.0
2	3	20.0	3	60.0	35	4	12.5	4	36.4
10	2	7.1	2	20.0	Farm F	1	2.6	1	7.1
11	0	0	0	0	39	0	0	0	0
16	1	6.7	1	16.7	40	1	4.0	1	11.1
					Farm W	5	41.4	4	33.3
					43	1	11.1	1	33.3
					44	5	14.3	5	38.5
					Farm B	2	11.1	2	33.3
					Farm H	0	0	0	0
					Farm M	3	13.6	2	22.2
					45	4	14.8	4	44.4
					46	1	3.8	1	9.1
					Farm GR	1	3.8	1	10.0
					47	5	17.2	3	30.0
					Farm GO	0	0	0	0
					Farm V	0	0	0	0
					48	2	7.4	2	25.0
Subtotal	7	6.8	7	20.0		36	8.1	32	20.0
			Study area total			43	7.8	39	20.0

[a]Numbers of trap nights and sites used are given in Table 44, page 422.

APPENDIX M

RESULTS OF THE SERUM SURVEY AMONG OPOSSUMS,

BY WEIGHT CLASS, SEX, AND TRAP AREA, 1973

Table 72. Results of the serum survey among opossums in the study area, 1973.[a]

Trap area	Age class / Wt. class / Sex	Juvenile 1 M	Juvenile 1 F	Juvenile 2 M	Juvenile 2 F	Subadult 3 M	Subadult 3 F	Adult 4 M	Adult 4 F	Adult 5 M	Adult 5 F	Adult 6 M	Adult 6 F	Adult 7 M	Adult 7 F	Total M	Total F	Total
		Weight classes are defined in Table 24, page 107																
1	RSN	-	-	-	-	-	1	1	0	-	-	-	-	-	-	1	1	2
	PRSP						0	0	1*							0	1*	1*
	DRSP						0	0	1†							0	1†	1†
3	RSN	-	-	-	1	-	-	-	1	1	-	-	-	-	-	1	2	3
5	RSN	-	1	-	-	-	1	2	-	-	1	-	-	-	-	2	3	5
8	RSN	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1
	PRSP										1*						1*	1*
11	RSN	-	1	-	-	1	1	-	-	-	-	-	-	-	-	1	2	3
13	RSN	-	-	-	-	-	-	-	-	-	-	-	0	-	-	-	0	0
	PRSP												1*				1*	1*
15	RSN	-	-	2	-	-	-	-	-	-	-	-	-	1	-	3	-	3
18	RSN	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	2	2
21	RSN	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2	2
22	RSN	-	-	-	-	-	-	1	-	-	0	-	-	-	-	1	0	1
	PRSP							0			1*					0	1*	1*

Table 72. continued.

Trap area	Age class / Wt. class / Sex	Juvenile				Subadult		Adult								Total		
		Weight classes are defined in Table 24, page 107																
		1		2		3		4		5		6		7				
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
23	RSN	-	1	1	-	-	-	-	1	-	-	-	-	-	-	1	2	3
24	RSN	-	-	-	-	1	-	-	-	-	1	-	-	-	-	1	1	2
25	RSN	-	-	1	-	1	1	1	-	-	-	-	-	-	-	3	1	4
27	RSN	-	-	-	-	-	-	-	-	1	1	1	-	-	-	2	1	3
28	RSN	-	-	-	-	-	0	-	1	-	-	-	-	-	-	-	1	1
	PRSP						1*		0								1*	1*
34	RSN	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	2	2
35	RSN	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	1
36	RSN	-	-	-	-	1	1	1	2	-	-	-	-	-	-	2	3	5
37	RSN	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1
38	RSN	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	2	2
39	RSN	-	-	-	-	-	-	-	-	1	-	-	1	-	-	1	1	2
45	RSN	-	2	1	-	-	-	-	-	-	0	-	-	-	-	1	2	3
	PRSP		0	0							1*					0	1*	1*
46	RSN	1	-	-	-	-	0	-	0	-	0	-	-	-	-	1	0	1
	PRSP	0					1*		1*		1*					0	3*	3*

Table 72. continued.

Trap area	Age class / Wt. class / Sex	Juvenile 1 M	F	2 M	F	Subadult 3 M	F	Adult 4 M	F	5 M	F	6 M	F	7 M	F	Total M	F	
		Weight classes are defined in Table 24, page 107																
47	RSN	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1
48	RSN	-	-	-	-	1	1	-	-	-	-	-	-	-	-	1	1	2
Subtotal																		
	RSN	1	6	5	1	6	7	6	9	3	7	1	2	1	-	23	32	55
	PRSP	0	0	0	0	0	2*	0	2*	0	4*	0	1*	0		0	9*	9*
	DRSP	0	0	0	0	0	0	0	1†	0	0	0	0	0		0	1†	1†
Weight class total																		
	RSN	7		6		13		15		10		3		1				55
	PRSP	0		0		2*		2*		4*		1*		0				9*
	DRSP	0		0		0		1†		0		0		0				1†
Total tested		7		6		15		18		14		4		1				65

[a]The sample(s) is (are) either rabies seronegative (RSN), presumptive rabies seropositive (PRSP *), or definitive rabies seropositive (DRSP †).

- = No samples tested.

APPENDIX N

RESULTS OF THE SERUM SURVEY AMONG OPOSSUMS BY WEIGHT CLASS, SEX, AND TRAP AREA, 1974

Table 73. Results of the serum survey among opossums in the study area, 1974.[a]

Trap area	Age class / Wt. class / Sex	Juvenile				Subadult		Adult								Total		
		Weight classes are defined in Table 24, page 107																
		1		2		3		4		5		6		7				
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
1	RSN	-	2	1	3	-	-	-	1	-	1	-	3	-	1	1	11	12
Farm C																		
	RSN	1	-	-	-	-	-	-	2	1	0	0	-	-	-	2	2	4
	PRSP								0	0	2*	1*				1*	2*	3*
	DRSP								1†	0	0	0				0	1†	1†
Farm K																		
	RSN	-	-	-	-	-	-	-	1	0	0	-	-	-	-	0	1	1
	PRSP								1*	0	2*					0	3*	3*
	DRSP								0	1†	0					1†	0	1†
2	RSN	-	-	-	-	-	-	-	0	-	-	1	-	-	-	1	0	1
	PRSP								0			0				0	0	0
	DRSP								2†			0				0	2†	2†
3	RSN	-	-	-	-	-	-	-	2	-	-	0	-	-	-	0	2	2
	PRSP								0			1*				1*	0	1*
4	RSN	0	-	-	-	-	-	-	3	-	1	0	-	-	-	0	4	4
	PRSP	1*							0		0	1*				2*	0	2*
5	RSN	-	-	-	-	-	-	-	1	-	0	1	1	-	-	1	2	3
	PRSP								0		1*	1*	0			1*	1*	2*

Table 73. continued.

Trap area	Age class / Wt. class / Sex	Juvenile: 1 M	1 F	2 M	2 F	Subadult: 3 M	3 F	Adult: 4 M	4 F	5 M	5 F	6 M	6 F	7 M	7 F	Total M	Total F	Total
		Weight classes are defined in Table 24, page 107																
6	RSN	1	-	-	-	-	-	-	1	-	1	-	-	-	-	1	2	3
	PRSP	0							1*		0					0	1*	1*
7	RSN	-	-	-	-	-	-	-	-	1	1	2	-	-	-	3	1	4
8	RSN	-	-	-	-	-	-	-	1	-	-	1	-	-	1	1	2	3
9	RSN	-	-	-	-	-	-	-	1	1	-	1	1	-	1	2	3	5
10	RSN	-	-	-	-	-	-	1	1	-	2	1	-	-	-	2	3	5
	PRSP							0	0		0	0				0	0	0
	DRSP							0	0		0	2†				2†	0	2†
11	RSN	-	-	-	-	-	-	-	0	2	1	2	-	-	0	4	1	5
	PRSP								0	0	0	0			1*	0	1*	1*
	DRSP								2†	0	0	0			0	0	2†	2†
12	RSN	1	-	-	-	-	-	-	-	1	-	-	-	-	1	2	1	3
13	RSN	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	1	2
14	RSN	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	2	2
15	RSN	-	-	-	-	-	-	-	-	1	-	0	-	-	-	1	-	1
	PRSP									0		1*				1*		1*

Table 73. continued.

Trap area	Age class / Wt. class / Sex	Juvenile				Subadult		Adult								Total		
		Weight classes are defined in Table 24, page 107																
		1		2		3		4		5		6		7				
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
16	RSN	-	-	-	-	-	-	-	1	0	-	-	-	-	-	0	1	1
	PRSP								0	1*						1*	0	1*
17	RSN	-	-	-	-	-	-	-	1	1	1	-	-	-	-	1	2	3
18	RSN	-	-	-	-	-	-	1	-	-	-	1	-	1	-	3	-	3
19	RSN	-	-	-	-	-	-	-	2	1	2	1	-	-	-	2	4	6
20	RSN	1	-	-	-	-	-	-	1	-	-	-	-	-	-	1	1	2
	PRSP	0							1*							0	1*	1*
22	RSN	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	2	2
23	RSN	-	-	-	-	-	-	-	0	-	2	-	-	-	-	-	2	2
	PRSP								1*		0						1*	1*
24	RSN	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	1
25	RSN	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1
26	RSN	-	-	-	-	-	1	-	1	0	-	0	-	-	-	0	2	2
	PRSP						0		0	1*		1*				2*	0	2*
27	RSN	-	-	-	-	-	-	-	-	-	-	3	1	-	-	3	1	4
28	RSN	-	-	-	-	-	-	-	-	-	2	-	1	1	1	1	4	5

Table 73. continued.

Trap area	Age class / Wt. class / Sex	Juvenile 1 M	1 F	2 M	2 F	Subadult 3 M	3 F	Adult 4 M	4 F	5 M	5 F	6 M	6 F	7 M	7 F	Total M	Total F	
		Weight classes are defined in Table 24, page 107																
29	RSN	-	3	-	-	-	-	-	1	1	-	-	-	-	-	1	4	5
	PRSP		0						0	1*						1*	0	1*
30	RSN	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	2	2
31	RSN	1	-	-	-	-	-	-	3	-	2	1	-	-	-	2	5	7
32	RSN	-	-	-	-	-	-	-	-	-	-	2	1	1	-	3	1	4
	PRSP											0	0	2*		2*	0	2*
33	RSN	-	-	-	-	-	-	-	-	-	1	1	1	-	-	1	2	3
	PRSP										0	1*	0			1*	0	1*
34	RSN	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	2	2
35	RSN	-	-	-	-	-	-	-	0	-	1	-	-	1	-	1	1	2
	PRSP								1*		0			0		0	1*	1*
36	RSN	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	1
37	RSN	-	-	-	-	-	-	-	-	-	0	-	1	-	-	-	1	1
	PRSP										0		0				0	0
	DRSP										1†		0				1†	1†
38	RSN	-	-	-	-	-	-	-	-	-	-	1	2	-	-	1	2	3
39	RSN	-	-	-	-	-	-	1	1	-	-	-	-	-	-	1	1	2

Table 73. continued.

Trap area	Age class / Wt. class / Sex	Juvenile 1 M	F	2 M	F	Subadult 3 M	F	Adult 4 M	F	5 M	F	6 M	F	7 M	F	Total M	F	
		Weight classes are defined in Table 24, page 107																
40	RSN	-	1	-	-	-	-	-	-	1	1	-	1	0	-	1	3	4
	PRSP		0							0	0		0	0		0	0	0
	DRSP		0							0	0		1†	1†		1†	1†	2†
41	RSN	-	-	-	-	-	-	-	-	-	-	0	-	1	-	1	-	1
	PRSP											1*		0		1*		1*
42	RSN	-	-	-	-	-	-	-	0	-	1	-	-	1	-	1	1	2
	PRSP								1*		0			0		0	1*	1*
43	RSN	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1	1	2
44	RSN	-	1	-	-	-	-	-	3	-	1	-	1	1	-	1	6	7
45	RSN	-	-	-	-	-	-	-	1	1	0	1	-	-	-	2	1	3
	PRSP								0	1*	1*	0				1*	1*	2*
	DRSP								0	0	1†	0				0	1†	1†
46	RSN	-	-	-	-	-	-	-	-	-	-	1	1	-	-	1	1	2
48	RSN	1	-	-	-	-	-	-	2	-	0	1	-	-	-	2	2	4
	PRSP	0							1*		2*	0				0	3*	3*
Subtotal																		
	RSN	6	7	1	3	-	2	4	37	14	25	23	15	7	5	55	94	149
	PRSP	1*	0	0	0	-	0	0	7*	4*	8*	8*	0	2*	1*	15*	16*	31*
	DRSP	0	0	0	0	-	0	0	5†	1†	2†	2†	1†	1†	0	4†	8†	12†

Table 73. continued.

Trap area	Wt. class	1	2	3	4	5	6	7	Total
	class	Juvenile		Subadult	Adult				
		Weight classes are defined in Table 24, page 107							
	Sex	M F	M F	M F	M F	M F	M F	M F	M F
Weight class total									
RSN		13	4	2	41	39	38	12	149
PRSP		1*	0	0	7*	12*	8*	3*	31*
DRSP		0	0	0	5†	3†	3†	1†	12†
Total tested		14	4	2	53	54	49	16	192

[a]The sample(s) is (are) either rabies seronegative (RSN), presumptive rabies seropositive (PRSP *), or definitive rabies seropositive (DRSP †).

- = No samples tested.

APPENDIX O

RESULTS OF THE SERUM SURVEY AMONG OPOSSUMS, BY WEIGHT CLASS, SEX, AND TRAP AREA, 1975

Table 74. Results of the serum survey among opossums in the study area, 1975.[a]

Trap area	Age class / Wt. class / Sex	Juvenile				Subadult		Adult								Total		
		Weight classes are defined in Table 24, page 107																
		1		2		3		4		5		6		7				
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
1	RSN	-	-	1	0	-	-	-	-	0	0	-	2	0	-	1	2	3
	PRSP			0	1*					1*	1*		0	1*		2*	2*	4*
2	RSN	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	-	2
3	RSN	-	-	-	-	-	-	-	1	-	0	2	-	1	-	3	1	4
	PRSP								0		1*	0		0		0	1*	1*
4	RSN	1	-	-	-	-	-	-	2	0	-	1	1	-	-	2	3	5
	PRSP	0							0	1*		0	0			1*	0	1*
5	RSN	-	-	-	-	-	-	-	3	-	1	1	-	1	-	2	4	6
	PRSP								1*		1*	0		0		0	2*	2*
6	RSN	1	-	1	1	-	-	-	-	-	2	-	-	-	-	2	3	5
	PRSP	0		0	0						1*					0	1*	1*
7	RSN	-	-	-	-	-	3	2	3	-	-	-	-	-	-	2	6	8
8	RSN	1	-	-	-	1	-	-	-	-	-	-	2	-	-	2	2	4
9	RSN	1	-	-	-	-	1	1	1	-	2	-	1	-	1	2	6	8
	PRSP	0					1*	0	0		0		1*		0	0	2*	2*

Table 74. continued.

Trap area	Age class / Wt. class / Sex	Juvenile				Subadult		Adult								Total		
		Weight classes are defined in Table 24, page 107																
		1		2		3		4		5		6		7				
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
10	RSN	1	-	-	-	-	-	-	-	-	3	-	0	-	-	1	3	4
	PRSP	0									2*		0			0	2*	2*
	DRSP	0									0		1†			0	1†	1†
11	RSN	-	-	-	-	-	-	-	1	-	1	-	-	1	-	1	2	3
12	RSN	-	-	1	-	3	1	-	-	-	-	-	1	0	-	4	2	6
	PRSP			0		0	0						0	1*		1*	0	1*
13	RSN	-	1	-	-	-	1	1	1	-	1	-	-	-	0	1	4	5
	PRSP		0				0	0	0		0				1*	0	1*	1*
14	RSN	-	-	-	1	2	2	-	0	-	2	-	-	-	-	2	5	7
	PRSP				0	0	0		1*		0					0	1*	1*
15	RSN	-	-	-	-	-	2	-	-	-	3	1	1	-	-	1	6	7
	PRSP						0				1*	0	0			0	1*	1*
16	RSN	-	-	1	-	-	-	0	0	-	1	-	2	-	0	1	3	4
	PRSP			0				1*	1*		0		0		1*	1*	2*	3*
	DRSP			0				0	0		0		1†		0	0	1†	1†
17	RSN	-	-	-	-	-	-	-	2	0	1	1	-	-	-	1	3	4
	PRSP								0		1*	0				1*	0	1*
18	RSN	-	1	-	-	-	-	-	-	0	1	-	0	-	-	0	2	2
	PRSP		0							1*	0		2*			1*	2*	3*

Table 74. continued.

Trap area	Age class / Wt. class / Sex	Juvenile 1 M	Juvenile 1 F	Juvenile 2 M	Juvenile 2 F	Subadult 3 M	Subadult 3 F	Adult 4 M	Adult 4 F	Adult 5 M	Adult 5 F	Adult 6 M	Adult 6 F	Adult 7 M	Adult 7 F	Total M	Total F	
		Weight classes are defined in Table 24, page 107																
19	RSN	-	-	-	-	-	-	-	1	-	4	-	1	-	-	-	6	6
20	RSN	-	-	1	1	-	-	-	1	-	1	1	2	-	-	2	5	7
	PRSP			1*	0				0		0	0	0			1*	0	1*
21	RSN	-	-	-	-	-	-	4	-	1	-	1	-	1	-	7	-	7
22	RSN	-	-	-	-	-	-	1	1	1	3	-	1	-	-	2	5	7
	PRSP							0	0	0	1*		0			0	1*	1*
23	RSN	-	-	-	-	-	-	-	-	-	1	-	1	1	-	1	2	3
24	RSN	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	2	2
25	RSN	-	-	-	-	-	-	-	0	-	1	-	-	-	-	-	1	1
	PRSP								1*		0						1*	1*
26	RSN	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	1
27	RSN	-	-	2	-	-	1	2	-	1	2	-	-	1	-	6	3	9
28	RSN	-	-	1	-	-	2	2	-	-	1	-	-	1	-	4	3	7
29	RSN	-	-	1	-	-	-	-	-	1	5	0	0	-	-	2	5	7
	PRSP			0						0	0	1*	1*			1*	1*	2*
30	RSN	-	-	-	-	2	1	-	-	-	1	-	1	1	1	3	4	7

Table 74. continued.

Trap area	Age class / Wt. class / Sex	Juvenile 1 M	Juvenile 1 F	Juvenile 2 M	Juvenile 2 F	Subadult 3 M	Subadult 3 F	Adult 4 M	Adult 4 F	Adult 5 M	Adult 5 F	Adult 6 M	Adult 6 F	Adult 7 M	Adult 7 F	Total M	Total F	Total
		Weight classes are defined in Table 24, page 107																
31	RSN	-	-	-	1	2	1	1	-	-	-	-	1	-	2	3	5	8
32	RSN	-	-	2	-	-	-	-	-	1	3	1	-	-	1	4	4	8
	PRSP			0						1*	0	0			0	1*	0	1*
33	RSN	-	-	-	-	-	-	-	-	-	2	-	1	2	-	2	3	5
34	RSN	-	-	-	-	-	-	-	-	1	-	-	-	-	1	1	1	2
35	RSN	-	-	-	-	1	1	-	1	-	2	-	-	1	-	2	4	6
36	RSN	-	-	1	-	2	-	1	-	1	0	-	1	-	-	5	1	6
	PRSP			0		0		0		0	1*		0			0	1*	1*
37	RSN	-	-	-	-	4	1	-	-	0	1	-	2	1	-	5	4	9
	PRSP					0	0			1*	0		0	0		1*	0	1*
38	RSN	-	-	-	-	-	2	1	3	-	-	-	1	-	-	1	6	7
39	RSN	-	1	1	-	-	-	1	1	-	2	-	1	-	-	2	5	7
	PRSP		0	0				0	1*		0		0			0	1*	1*
40	RSN	3	1	-	-	-	-	-	-	0	1	-	-	-	-	3	2	5
	PRSP	0	0							1*	0					1*	0	1*
41	RSN	-	-	-	-	-	-	-	1	-	1	0	-	1	-	1	2	3
	PRSP								0		0	1*		0		1*	0	1*

Table 74. continued.

Trap area	Age class / Wt. class / Sex	Juvenile 1 M	Juvenile 1 F	Juvenile 2 M	Juvenile 2 F	Subadult 3 M	Subadult 3 F	Adult 4 M	Adult 4 F	Adult 5 M	Adult 5 F	Adult 6 M	Adult 6 F	Adult 7 M	Adult 7 F	Total M	Total F	Total
		Weight classes are defined in Table 24, page 107																
42	RSN	-	-	1	1	-	-	-	-	-	2	1	2	1	-	3	5	8
	PRSP			0	0						0	0	0	1*		1*	0	1*
43	RSN	-	1	-	-	-	-	1	-	-	1	-	1	0	-	1	3	4
	PRSP		0					0			0		0	1*		1*	0	1*
44	RSN	-	-	-	-	-	-	-	1	-	1	-	1	-	-	-	3	3
	PRSP								0		1*		0				1*	1*
45	RSN	1	-	-	-	-	-	-	-	-	1	1	-	-	-	2	1	3
46	RSN	-	-	-	-	-	-	1	0	-	5	-	1	1	-	2	6	8
	PRSP							0	1*		0		0	0		0	1*	1*
47	RSN	-	-	-	-	1	1	-	1	-	3	-	1	-	-	1	6	7
	PRSP					1*	0		0		0		1*			1*	1*	2*
48	RSN	-	-	-	-	-	-	-	1	-	3	-	-	-	-	-	4	4
	PRSP								0		0						0	0
	DRSP								0		1†						1†	1†
Subtotal																		
	RSN	9	5	14	6	18	20	19	27	7	65	13	30	15	6	95	159	254
	PRSP	0	0	1*	1*	1*	1*	1*	6*	7*	10*	2*	5*	4*	2*	16*	25*	41*
	DRSP	0	0	0	0	0	0	0	0	0	1†	0	2†	0	0	0	3†	3†

Table 74. continued.

Trap area	Age class	Juvenile		Subadult	Adult				
	Wt. class	Weight classes are defined in Table 24, page 107							
		1	2	3	4	5	6	7	Total
	Sex	M F	M F	M F	M F	M F	M F	M F	M F
Weight class total									
RSN		14	20	38	46	72	43	21	254
PRSP		0	2*	2*	7*	17*	7*	6*	41*
DRSP		0	0	0	0	1†	2†	0	3†
Total tested		14	22	40	53	80	52	27	298

[a]The sample(s) is (are) either rabies seronegative (RSN), presumptive rabies seropositive (PRSP *), or definitive rabies seropositive (DRSP †).

- = No samples tested.

APPENDIX P

RESULTS OF THE SERUM SURVEY AMONG OPOSSUMS, BY WEIGHT CLASS, SEX, AND TRAP AREA, 1976

Table 75. Results of the serum survey among opossums in the study area, 1976.[a]

Trap area	Age class / Wt. class / Sex	Juvenile				Subadult		Adult								Total		
		Weight classes are defined in Table 24, page 107																
		1		2		3		4		5		6		7				
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
1	RSN	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	1
2	RSN	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	1
10	RSN	-	-	-	-	1	-	-	-	-	-	1	-	-	-	2	-	2
11	RSN	-	-	-	-	-	-	-	1	1	-	-	-	-	-	1	1	2
16	RSN	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	1
35	RSN	-	-	-	-	-	1	-	1	-	2	-	-	-	-	-	4	4
	PRSP						0		1*		0						1*	1*
Farm F	RSN	-	-	1	1	-	-	-	1	-	-	-	0	1	-	2	2	4
	PRSP			0	0				0				1*	0		0	1*	1*
39	RSN	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1
40	RSN	-	-	-	-	1	0	-	-	-	1	-	-	-	1	1	2	3
	PRSP					0	1*				0				0	0	1*	1*
Farm W	RSN	-	-	-	-	-	2	-	-	-	-	-	-	-	1	-	3	3

Table 75. continued.

Trap area	Age class / Wt. class / Sex	Juvenile				Subadult		Adult								Total		
		Weight classes are defined in Table 24, page 107																
		1		2		3		4		5		6		7		Total		
		M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	
44 RSN		-	-	-	-	1	-	-	2	-	2	-	-	-	-	1	4	5
Farm B RSN		-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	2	2
Farm H RSN		-	-	1	-	-	-	-	-	-	-	-	1	-	-	1	1	2
Farm M RSN		-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	2	2
45 RSN		-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1
46 RSN		-	-	-	-	-	-	1	-	-	2	-	-	-	-	1	2	3
Farm GR RSN		-	-	1	-	-	-	-	-	-	-	-	0	-	-	1	0	1
PRSP				0									1*			0	1*	1*
47 RSN		-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	3	3
Farm GO RSN		-	-	1	-	-	-	-	-	-	-	1	1	-	-	2	1	3
Farm V RSN		-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	1

Table 75. continued

Trap area	Age class / Wt. class / Sex	Juvenile 1 M	F	2 M	F	Subadult 3 M	F	Adult 4 M	F	5 M	F	6 M	F	7 M	F	Total M	F	
						Weight classes are defined in Table 24, page 107												
48	RSN	-	-	-	-	1	1	-	-	-	-	-	2	-	-	1	3	4
Subtotal																		
	RSN	-	-	4	1	5	5	2	7	1	12	2	6	1	3	15	34	49
	PRSP			0	0	0	1*	0	1*	0	0	0	2*	0	0	0	4*	4*
Weight class total																		
	RSN	-		5		10		9		13		8		4				49
	PRSP			0		1*		1*		0		2*		0				4*
Total tested		-		5		11		10		13		10		4				53

[a]The sample(s) is (are) either rabies seronegative (RSN), presumptive rabies seropositive (PRSP *), or definitive rabies seropositive (DRSP †).

- = No samples tested.

APPENDIX Q

A CONSIDERATION OF CARRION FEEDING IN RABIES TRANSMISSION AND ITS RELATIONSHIP TO RABIES ECOLOGY

APPENDIX Q

A CONSIDERATION OF CARRION FEEDING IN RABIES TRANSMISSION AND ITS RELATIONSHIP TO RABIES ECOLOGY

It was noted in the final section of the discussion that one feasible method for rabies maintenance is the presence of subclinical rabies infections among the major host species of clinical rabies and/or other inapparent reservoir species. Such infections would permit infected animals to carry the virus throughout their lives without developing the clinical disease which normally results in death. If the rabies virus is maintained in this manner, then the question of animal-to-animal transmission becomes very important. In the past the aberrant behavior and vicious biting attacks associated with clinical rabies were considered essential for most rabies transmission, particularly among terrestrial carnivores. In recent years other methods have been discovered to account for some rabies transmission in the absence of the clinical disease. One such method for the natural circulation of rabies which has not been extensively evaluated is carrion feeding. This appendix represents a synthesis of the ideas surrounding carrion feeding as a mode of rabies transmission and the relationship of this concept to the data gathered in this and other studies on wildlife rabies ecology.

The data of the present study suggest that the level of reported rabies cases in the study area was not sufficient to expose the large number of cats and opossums which gave some evidence of prior contact with the rabies virus, i.e., rabies seropositive cats and opossums. The exposure of opossums and cats to rabies may have resulted from the ingestion of rabies infected tissue. While such feeding may have involved the consumption of animals which had died of clinical rabies, an alternative mode would involve feeding on rabies infected animals which had died of other causes such as starvation, diseases other than rabies, or accidental deaths due to collisions with automobiles or farm machinery. The acquisition of a rabies infection by carrion feeding would not be limited to the consumption of rabies infected skunks. Since one opossum was found with rabies antigen in its salivary gland, a carrion feeding circulation of rabies virus could involve both intra- and interspecific scavenging by a variety of omnivorous and carnivorous species.

If rabies, a disease of the nervous system, is transmitted by carrion feeding, it would not be totally unique. In recent years considerable evidence has indicated that kuru, a slow degenerative disease of the human nervous system caused by a virus-like agent, is transmitted during ritual cannibalism (Gajdusek 1977:949). There is evidence to suggest that infection may have taken place through contamination of body surfaces during the act of cannibalism. Gajdusek (1977:

957-959) presented arguments to suggest that other slow degenerative nervous system diseases may be spread, in part, by the oral route. He noted that mink on certain commercial ranches developed transmissible mink encephalopathy (TME) after they had been fed carcasses of scrapie-infected sheep, and he postulated that these two diseases may be caused by the same disease agent. He suggested that TME may have originated as mink fed on scrapie-infected sheep carcasses. While these findings may seem remote from the epizootiology of rabies, the facts suggesting that some nervous system diseases are transmitted during the act of carrion feeding and/or the ingestion of infected tissue provide hypothetical models for a carrion feeding transmission cycle for wildlife rabies.

A carrion feeding mode of rabies transmission is dependent on demonstrating that an infection can develop by the ingestion of rabies infected tissue. Soave (1966:45) reported that some laboratory mice which ate rabies infected brain tissue developed clinical rabies. The occurrence of clinical rabies was not dependent on the presence of a mouth wound. He also stated that the investigation indicated:

> The rabies virus remains viable in the brain of dead mice for at least eight days when the brain was held at 25° C and 20 days at 10° C—a sufficient period of time for the carcass of an animal dying of rabies to become a source of virus for other animals.

Fischman and Ward (1968:135) infected neonatal mice with rabies, and noted that some of these young mice were found missing after the inoculation, probably as a result of cannibalism by the mother. They then found that:

> Seven to 10 days later deaths among mother mice began to appear. Throughout many experiments using neonatal mice, deaths due to rabies were not seen among mother mice unless their infant mice were first found missing.

The authors also noted that:

> Large doses of virus were required to infect animals orally. However, dying wild animals might easily contain such concentrations of virus in their brains as well as other tissues (Fischman and Ward 1968:136).

Fischman and Schaeffer (1971:79,84) found that rabies infection of the oral cavity in mice and hamsters resulted when rabies infected tissue was consumed. The authors concluded that:

> Infection of the oropharyneal-intestinal tissues did not represent centrifugal spread but reflected the site of invasion following infection by the oral portal.

Correa-Giron et al. (1970:206-270) found that different strains of the rabies virus differed in their ability to cause rabies mortality among laboratory mice. They also reported that after feeding rabies infected brain tissue to mice:

> Rabiesvirus was isolated from the stomach and intestines of mice sacrificed six hours after ingestion of infected tissue, suggesting that the bovine strain of rabiesvirus used resisted <u>in vivo</u> the action of mouse digestive juices for the time period (Correa-Giron et al. 1970:213).

The authors concluded that:

> Following oral administration, rabies virus can initiate infection through the buccal and lingual mucosae, taste buds, lungs, or through the intestines (Correa-Giron et al. 1970:214).

Bell and Moore (1971:179) reported that six of 18 skunks which were each fed one rabies infected mouse died of rabies. The serum analyses of 14 skunks after exposure revealed that none had formed rabies SN antibodies at a 1:10 dilution. None of 65 cats which consumed one or more rabies infected mice developed rabies.

Ramsden and Johnston (1975:320-323) found that two of 11 red foxes developed clinical rabies after ingesting rabies infected white mice, and two other foxes developed rabies antibody titers sufficient to resist an intramuscular rabies challenge. Similar results were obtained among striped skunks. While 10 of 13 immature skunks developed clinical rabies after ingesting rabies infected white mice, in two other trails among immature and adult striped skunks, none of 11 animals fed infected mice developed rabies, but one adult formed rabies antibodies. The authors suggested that:

> Occurrence of SN antibody following oral exposure may account in part for presence of SN antibody at low levels in carnivores in rabies enzootic areas (Ramsden and Johnston 1975:320).

Some of the data from these laboratory studies may not be directly applicable to a field situation. Some of the studies were based on the consumption of only brain tissue from clinically rabid animals, and in some cases the challenge virus standard (CVS) type of rabies virus was used. Fischman and Ward (1968:137) stated that:

> The CVS rabies virus . . . is a highly neurogenic and mouse adapted strain. Fixed viruses generally assume a high state of virulence for the animals in

> which they are fixed, ... Street rabies viruses have a broader tissue tropism, are generally found with lower titers, and may have considerably longer incubation periods. In a more natural host-parasite relationship, virus invasion might take place without resulting in immediate death.

Therefore, it is possible that a different pattern of oral rabies infection would occur following the ingestion of non-neural tissue containing wild-type rabies virus.

It is a well established fact that the rabies virus can and does infect a wide variety of tissues in the clinically rabid animal. Schneider (1975:274) remarked that:

> There is hardly any organ which at one time or another cannot be shown to yield rabies virus or antigen if a careful enough search is made. Virus thus obtained will usually be present in low titer only.

Specifically, parts of the respiratory and urinary systems may become infected (Schneider 1975:278-280, Debbie and Trimarchi 1970:501). Johnson (1966:29) found rabies virus in the pectoral muscles, intestinal mucosa, lungs, kidneys, salivary glands, and brain of a naturally infected striped skunk. Smith et al. (1972:1495) found that rabies virus antigen was present in the nerve tissue of the skin in mice inoculated with rabies.

Debbie and Trimarchi (1970:501-504) found rabies antigen in a wide variety of tissues from clinically rabid red foxes. Besides the brain and spinal cord, the only tissue consistently found to contain rabies antigen was the esophagus. Within the esophagus the antigen was primarily in the connective tissue of the submucosa and/or between the muscle layers, but antigen was noted in the epithelial cell lining of a third (4/12) of the foxes examined. The virus was also found in the stomach (6/12 foxes) and the small intestines (3/12 foxes). The urinary bladder from 10 of the 12 foxes contained rabies virus, and mice inoculated with urine from one such fox died of rabies.

These data indicate that a scavenger feeding on a rabies infected animal could ingest infective rabies virus without consuming the brain or spinal cord. Considering the intense manner in which scavengers often feed, respiratory infection could occur concurrently with infection via the digestive system. Overall, the feasibility of carrion feeding in rabies transmission was summarized by Ramsden and Johnston (1975:323) who stated "ingestion of rabies infected carcasses by carnivores has been proven . . . to be a possible means of rabies transmission."

A carrion feeding mode of intra- and interspecific rabies transmission is also dependent on a significant level of scavenging by the species involved in rabies circulation. Many wildlife studies have dealt with the food habits of wildlife species, and much data are available in this area.

It is interesting to note that most of the major terrestrial rabies hosts feed in a predator/scavenger manner. In Tanzania Rweyemanu et al. (1973:22-23) reported on the species composition among reported rabies cases from 1966 through 1970. While the dog was the major rabies host (318 cases), the wild animals most commonly found to be rabid were jackals and hyenas, with 12 reported cases for each group. These two groups of wild animals feed, to some extent, on carrion (Ewer 1973:149-152, 202-204).

Animals which are predominantly predators or herbivores are infrequently found to be rabid. The majority of wildlife species which are mainly herbivorous belong to the mammalian orders of Rodentia and Lagomorpha. Winkler (1972b:565) noted that clinical rabies cases among rodents and lagomorphs accounted for only a small but persistent segment of the reported rabies cases in the United States. However, data based on experimental rabies inoculations have indicated that some common rodents are susceptible to rabies infection, may develop aggressive behavior when clinically rabid, and shed rabies virus in their saliva (Winkler et al. 1972b:101-102). The lack of clinical rabies among rodents may not be completely dependent on a lack of contact with clinically rabid animals. Johnston and Beauregard (1969:366) reported that the contact rate between porcupines (Erethizon dorsatum) and rabid red foxes was apparently quite high in Ontario, but there had not been any reported rabies cases among porcupines.

On the other side of the feeding spectrum, those groups of animals which are predominantly carnivorous are likewise involved in reported rabies cases in only a sporadic way.

Regarding such Mustelidae as the mink and weasel, Ewer (1973:172) wrote:

> The weasels as a whole can thus be said to be truly carnivorous: they are specialist killers of small mammals and birds, making little use of invertebrates or vegetable foods and showing little seasonal change in diet.

Similarly, the predatory cats seem to prefer freshly killed game, and Ewer (1973:205) stated that:

> There are no largely vegetarian or even omnivorous felids: alone amongst the families of the Carnivora the Felidae are all essentially predators.

Reported raccoon rabies cases were rare in the study region with only three cases among the 3,651 reported cases. Ewer (1973:163-165) noted that raccoons feed predominantly on plant material, small rodents, and invertebrates. Gander (1966:87) observed raccoons in his back yard and noted that they did not feed on tainted meat, a practice not observed with gray foxes or spotted skunks. It is interesting to note that some raccoon rabies outbreaks in Florida have followed major destruction of wildlife habitat which may have resulted in radical changes in the feeding behavior of raccoons. Bigler et al. (1973:334) stated that some Florida raccoons became "beggars and scavengers" as they retreated into the areas left to them.

Between those animals which are highly carnivorous or highly herbivorous, there is a group of species which may be considered as omnivorous in the sense that they eat both plant material and actively prey on certain invertebrates and vertebrates. In the study region the two major animal categories among reported rabies cases were foxes and dogs. Trapp and Hallberg (1975:170-171) noted that the gray fox was an "opportunistic consumer" and would eat arthropods, plants, reptiles, and mammals. Similarly, Ables (1975:226) stated that the red fox of North America was an opportunistic feeder which would take any acceptable food, including small rodents, rabbits, wild fruit and berries, and insects.

Foxes and free-roaming domestic dogs may feed occasionally on carrion. Carrion occurred in approximately 7 percent (2/29) of the red fox stomachs examined in Wisconsin (Karpuleon 1957:592). Among red foxes in Missouri, carrion was the fifth most important category of food (Korschgen 1959:170). Studies among gray foxes have shown that the volume of carrion in the diet can range from 0 to 11.2 percent (Trapp and Hallberg 1975:170). Scott and Causey (1973:262) found that "feral dogs apparently were not reluctant to consume carrion since they were often caught in traps baited with decayed meat." Nesbitt (1975:395) found that a pack of free-roaming dogs in Illinois fed on a variety of food items which included road-killed animals and carrion.

Striped skunks also appear to feed on carrion and may, under certain circumstances, be cannibalistic. In Illinois a study of striped skunk food habits indicated the consumption of striped skunks and domestic cats, but the remains of striped skunks were considered to be "entirely" the result of self-grooming and chewing off of limbs caught in traps (Verts 1967:74,200). The author concluded that "no evidence of cannibalism was found." However, Wade-Smith and Richmond (1975:582) reported some cannibalism among captive striped skunks, and Allen and Shapton (1942:63) found one striped skunk in a den with another skunk which was dead and partly eaten. Verts (1967:73) presented information indicating that the percent frequency of occurrence for carrion in striped skunk diets ranged from 0 to 14.2 percent. While studying fox rabies in Virginia, Carey (1974:144) noted that the degree to which foxes consume dead foxes is unknown, "but it is likely that skunks and other scavengers would."

Data from the serum survey suggest that both domestic cats and opossums were exposed to rabies. In a strict sense, free-roaming domestic cats may not be considered as scavengers. However, the fact that many cats entered the traps used during the study which were baited with canned meat products indicates some level of opportunistic feeding by this species.

Opossums are active scavengers and may be cannibalistic. When plant and invertebrate food sources become scarce, opossums "readily become scavengers" (Lowry 1974:60). Reynolds (1945:369) suggested that carrion feeding was responsible for the occurrence of "the flesh of cottontails, house cats, opossums, squirrels, raccoons, and skunks" in the diet of opossums. Reynolds (1953:90) also stated that the opossum may have a false reputation as being highly cannibalistic, but he noted that they do "occasionally eat one another." Cannibalism may be the result of extreme hunger or some dietary deficiency. In a laboratory study, Barr (1961:33,37-38) found that some young opossums may have been eaten by their mother or littermates, and he noted that such behavior probably resulted from an anemic condition.

Some supportive evidence for the dominance of predator/scavenger animals in wildlife rabies is found among the few cases of birds infected with rabies. In an Iowa study, Gough and Jorgenson (1976:392-394) found some rabies seropositive birds among several predatory species and in such scavengers as the crow and raven (*Corvus corax*). Irvin (1970:343) summarized several reports on rabies among birds, and he noted that rabid birds in Europe were principally *Falco* spp. and *Buteo* spp. with some cases occurring among vultures. Some birds of prey may be immunologically suited to resist a large oral rabies infection. Jorgenson and Gough (1976:445-447) observed that a great horned owl (*Bubo virginianus*) would eat a rabies infected spotted skunk carcass, and this owl later showed evidence of rabies antigen in the pharynx and brain. The owl developed rabies antibodies and did not show signs of clinical rabies. Bird to bird transmission of rabies is probably rare (Gough and Jorgenson 1976:394). It is also unlikely that such interspecific methods of rabies transmission as aerosol, urinary, or biting would account for rabies infection among scavenging birds. The most likely means of rabies transmission between mammals and birds would be predation and carrion feeding, both of which imply an oral route of infection.

While data regarding rabies infection among birds suggest both a predatory and carrion feeding mode of transmission, it does not appear that predation alone could account for the widespread dissemination of rabies among the major terrestrial wildlife species in an area such as northeastern Tennessee. In the temperate regions of North America there is little evidence that medium-sized carnivores or omnivores prey extensively on other carnivores or omnivores. Considering such species as the red and gray foxes, striped skunk, opossum, cat, dog, and raccoon, the extent of predation within the group may be quite small. The bioenergetic factors present in any model of a food chain suggest that animals on one trophic level must feed primarily on food material from a lower trophic level.

An analysis of the feeding behavior of certain medium-sized omnivores may help to explain the most recent change observed in the major rabies host in the study region, a shift from the fox to the skunk. Furthermore, the varying degree of selectivity in the items consumed as carrion among foxes and skunks could account for the nonreversible shift from a period of numerous rabid foxes to a time of rabies predominantly among skunks.

The remarkable defense mechanism of skunks provides successful protection against most predators. While some predators may prey on skunks when near starvation, Verts (1967:121) stated that "no evidence of predation on striped skunks was noted in northwestern Illinois" and only "indirect evidence of avian predation" was found. Ables (1975:227) noted that certain prey species, especially insectivores and mustelids, are disliked by the red fox as dietary items and such animals are frequently killed but left uneaten unless other preferred foods are not available. Errington (1935:198) found skunks to constitute less than 1 percent of the animal species utilized by mid-western foxes, and Korschgen (1959: 171) found skunk remains in only 0.4 percent of 1,006 red fox stomachs collected in Missouri.

Opossums also seem to be less desirable prey for larger predators. Reynolds (1953:94) commented that the flesh of opossums is apparently "unpalatable to predators. I have yet to find a single animal that consistently feeds on opossums." Fitch and Shirer (1970:186) found a dead adult male opossum and stated that it had extensive mechanical injury suggesting that it had been attacked by a dog or coyote, but none of the carcass had been eaten. McManus (1974:3) noted that few predators seem to take opossums with regularity.

Overall, food habit studies suggest that skunks and opossums are generalized scavengers which might readily feed on the carcasses of foxes, skunks, opossums, and other animals which may have died of rabies or a host of other causes. However, such predator/scavengers as domestic dogs and foxes might pass up the carcass of a dead skunk or opossum. It is possible that skunks, opossums, or other animals infected with rabies might die in small crevices or dens inaccessible to foxes and dogs, but not closed to scavenging by skunks, opossums, or even domestic cats. It is also possible that some rabies infected carcasses would be consumed by the more abundant scavengers such as skunks and opossums before larger predator/scavengers such as dogs and foxes located the carcass.

Based on the hypothesis of this study, the emergence of skunk rabies would have begun as skunks fed on the carcasses of rabies infected foxes. The fact that the earliest skunk rabies cases were reported in counties which had a persistent fox rabies problem is consistent with this hypothesis. If the fox-to-fox chain of rabies infection should be broken after the disease became established among skunks, it is possible that the reluctance of foxes to feed on dead skunks could have prevented the reintroduction of rabies into the fox population.

Opossums may have been continually infected with rabies during the years of dog, fox, and skunk rabies by feeding on infected carcasses. The opossum is a scavenger with an evolutionary history of approximately 80 million years (Reynolds 1953:88), and it is understandable that the species has developed an innate resistance to clinical rabies.

The serum survey data suggest that rabies exposure among opossums in the study area was quite high, but the exact source of this rabies exposure remains unclear. This study would hypothesize that opossums are infected with rabies primarily through carrion feeding. Following infection opossums would carry the virus asymptomatically. These infections would not lead to clinical rabies with the subsequent dissemination by vicious biting attacks. However, to the extent that opossums and other scavengers acquire the rabies virus by feeding on the remains of rabies infected animals, the opossum would not be a "dead-end" for the rabies virus. In fact, the opossum may form an important link in the circulation of rabies in the study region.

The proposed carrion feeding method of rabies transmission suggests a reason for the disparity between the number of clinically rabid canids and felids, both wild and domestic, reported in the study region. The available data show a combined total of 2,797 dogs and foxes were reported rabid over the same time period in which only 176 cats and bobcats were reported rabid (Table 9, page 54). As a group the Felidae are better able to secure fresh prey and rely less on carrion than most members of the family Canidae. The data presented in Table 48, page 331, indicate that canids, as a group, have both higher and lower susceptibilities to rabies than the two felids found in the study region, and thus relative resistance to rabies would not seem to account for the fact that almost

16 times as many canids were reported rabid as felids in the study region. Irvin (1970:335) stated that on a world-wide basis rabies cases among wild Felidae are uncommon while rabies among the Canidae are widespread and common. This study would hypothesize that the difference in the extent of carrion feeding between canids and felids is responsible for the degree of involvement of these animals in the epizootiology of rabies.

A carrion feeding method for rabies transmission may be used to explain the annual cycle of reported rabies cases. In many parts of North America most reported rabies cases occur during or soon after the coldest months of the year. In the present study most rabies cases were reported during the March-April period (Fig. 20, page 91), the months immediately following the harsh winter months. If some time is allowed for varying incubation periods, it would appear that many rabies infections are acquired or reactivated during the colder months of the year. A carrion feeding mode of rabies transmission could account for this phenomenon.

During the winter months, particularly the late winter months, food for most wildlife species becomes scarce. During winter omnivorous mammals cannot rely on the numerous plant food items utilized at other times of the year. Some animals may die of starvation, and both carnivores and omnivores may feed on these carcasses. Hamilton (1936:245) stated that "during times of stress much of the skunk's food is composed of carrion." Verts (1967:74) stated that the most intensive predation by skunks on small mammals occurred in late winter and spring. It is likely that any carcasses found during foraging would be eaten. Considering that carrion feeding is a possible means of acquiring a rabies infection, an increase in such feeding during late winter could account for the upsurge of reported rabies cases during or soon after the late winter-early spring period.

A second factor which could influence the increase of reported rabies cases during late winter is the prolonged survival of the rabies virus in infected tissue at lower temperatures. Burkel et al. (1970:497-498) found that rabies virus could be detected in rabid skunk carcasses by the mouse inoculation test for longer periods of time at lower temperatures. These skunk carcasses were intended to represent road-killed animals, and as such they would also constitute sources of rabies virus for carrion feeders. At the lowest temperature tested, 11° C (52° F), the mouse inoculation test gave positive results for periods between 24 and 48 hours. Soave (1966:45) also found that the rabies virus remained viable in dead tissue longer when maintained at lower temperatures. Therefore, carrion feeding on rabies infected animals during the summer would have a much smaller chance of resulting in a disease producing infection, but carrion feeding during the cold winter months might not only be more frequent but also have an increased probability of containing infective virus. These considerations may be important in the epizootiology of rabies in arctic areas where scavenging is common and the virus might persist over extended periods of time in dead animals.

Some authors have associated a late winter-early spring upsurge in wildlife rabies cases to increased animal contact during the annual breeding season (Held et al. 1967: 1012, Webster et al. 1974:165-166, Parker 1975:49). Verts (1967:106) suggested that the breeding season among striped skunks may not vary greatly throughout the range of the species. As the breeding season may relate to the peak in the annual incidence of skunk rabies, it is interesting to note that no strong seasonal pattern seemed to exist in the occurrence of 42 rabid skunks reported in Florida during the 1951-1973 period (Prather et al. 1975:82-83). However, fox rabies cases did occur predominantly during the first five months of the year (Prather et al. 1975:58,60). In a state such as Florida with relatively mild winters, there may not be severe late winter mortality and increased carrion feeding behavior. These considerations merit the tentative suggestion that an annual peak of skunk rabies cases as noted in the study area may be related to factors other than contact associated with the breeding season. A carrion feeding mode of rabies transmission represents one feasible explanation for this phenomenon.

A carrion feeding mode of rabies transmission may be considered in relation to the landscape epizootiology of rabies in the study area. The reported rabies cases in the study area did appear to be clustered. While the exact reasons for these geographical foci could not be determined, one possible explanation is that the focal areas were, in some way, less than suitable skunk habitat. Clinical rabies among skunks may have occurred in areas which created significant hardships on skunks either through a lack of food, suitable den sites, or a host of other environmental factors. If the geographical foci of rabid skunks were related to areas where skunks were experiencing stress, then the feeding behavior of skunks in these areas could have been altered to the point where carrion assumed a greater role in the diet. In areas of poor skunk habitat, skunk mortality might be expected to increase, and the surviving skunks might consume these carcasses and thereby risk acquiring a rabies infection. Den sites might be limited and communal denning could become common with the increased potential for rabies transmission by cannibalism. While studying the winter den ecology of Michigan striped skunks, Allen and Shapton (1942:65) found one skunk in a den near the fresh remains of another skunk.

One interesting and uncertain aspect of a carrion feeding mode of rabies transmission is the dose-response consideration. Once a rabies infected animal dies, the rabies virus as an obligate intracellular organism cannot survive long. Beginning soon after the time of death, the amount of infective virus would start to decline. This principle was used by Pasteur in developing the first rabies vaccine. This vaccine consisted of an emulsion prepared from the spinal cords of rabbits infected with rabies. The spinal cords were allowed to dry, and the cords which dried the longest stimulated antibodies with less risk of disease. This process may have an analogy in the carrion feeding transfer of rabies by the ingestion of rabies infected tissue. If a scavenger found the rabies infected carcass at an appropriate time after death and consumed the tissue, the carrion feeder might receive a viral dose sufficient to stimulate rabies antibody production with little risk of developing clinical rabies. This infected scavenger might carry the rabies virus in some non-neural tissue during its life and become the source of rabies infection for another scavenger upon death.

At the present time there are no field data to support the theory outlined above. Parker (1962:276) theorized that skunks which received a small dose of rabies virus might carry the infection for many months and serve as potential reservoirs of the virus. There is some experimental evidence to indicate that lower doses of rabies virus are less likely to produce clinical rabies. Sikes (1962:1043) found that among skunks, but not foxes, rabies mortality after experimental infection varied directly with the amount of virus given, and none of the skunks given the smallest inoculum died of clinical rabies. Similar data were reported by Parker and Wilsnack (1966:35), Constantine and Woodall (1966:29), and Black and Lawson (1970:310). Some animals which survive their initial exposure to rabies may develop rabies specific antibodies. Data presented by Ramsden and Johnston (1975:318) indicated that after an oral exposure to rabies virus, some red foxes and striped skunks developed antibody levels sufficient to resist an intramuscular rabies challenge. Therefore, it is conceivable that the carcass of a rabies infected animal could constitute a potential source of an immunizing rabies infection.

Rabies transmission by carrion feeding may be considered in relation to the population density of the major host species and the initiation of rabies epizootics. While the association of high host population densities with the initiation of rabies epizootics is not clear in all instances, some rabies outbreaks, particularly among foxes, appear to occur at times of abnormally high population levels of the major host species (Rausch 1958:255, Marx and Swink 1963: 171-172). If the major rabies host is a predator/scavenger such as the dog, fox, or skunk, increasing population levels may force some members of the population into an increased reliance on carrion feeding. Such adverse population densities may also increase or initiate cannabalistic behavior within the major host species. In the areas where numerous clinical rabies cases do erupt at times of overpopulation among the major rabies host, the time interval between the death of a rabies infected animal and the consumption of the carcass by a carrion feeder may be quite short. The rapid discovery and consumption of rabies infected carcasses would be likely to transmit a large dose of the virus and increase the chances of producing clinical rabies. Therefore, in areas of high host species density, the stresses of overcrowding and the short time interval before the consumption of rabies infected carcasses might combine to initiate a rabies epizootic.

In contrast to the concept of rabies outbreaks during periods of host species overpopulation, the present study indicated that upsurges of clinical rabies among skunks could not be conclusively linked to an overabundance of skunks. Furthermore, the limited data of the study suggested that the emergence of skunks as the major rabies host followed a major decline in the skunk population. It is possible to hypothesize that this apparent decline in the skunk population was a response to some type of environmental stress. Major habitat destruction, a reduction in available food, or a host of other adverse environmental factors could have created stresses which would have reduced the ability of skunks to resist the development of clinical rabies. Starvation and increased skunk mortality could have created more carrion feeding behavior among surviving skunks. An increase in both adverse environmental factors and carrion feeding may have produced the periodic outbreaks of skunks rabies observed in the study area.

These considerations regarding the initiation of rabies epizootics presuppose that the rabies virus was not introduced into the host population as the adverse environmental conditions developed, but that the virus was a persistent member of the ecosystem and circulated as a nonlethal infection during times when the animal populations are in balance with the environment. The hypothesis suggests that in healthy populations the rabies virus may be widely disseminated by means of carrion feeding transmission. Carcasses of rabies infected animals might normally be found at time intervals conducive to the ingestion of an immunizing dose of virus, and an adequate food supply would further enhance the ability of infected animals to form rabies antibodies and resist clinical disease. The rabies virus acquired by carrion feeding might persist in the intestines, lungs, or oral cavity in such a manner that nerve tissue was not infected. This persistent infection might simply represent the long incubation period of a healthy animal which receives a small rabies dose orally, but in such short-lived animals as opossums, striped skunks, and foxes an extended incubation period could virtually eliminate the occurrence of overt disease.

The consideration of carrion feeding as an important means of rabies transmission is not intended as a complete alternative to bite transmission via infective saliva. However, bite transmission is normally associated with the aberrant behavior of clinical rabies immediately prior to the death of the host. Such bite transmission is obviously an important means of transmission during epizootics when new susceptible hosts are abundant. However, rabies epizootics may be relatively short in duration and the inter-epizootic periods may be characterized by few, if any, reported rabies cases. A long period of enzootic or sporadic clinical rabies cases suggests that bite transmission by clinically rabid animals may not be the most important, long-term means of rabies transmission.

During the interepizootic period or at times of low host populations, rabies transmission by biting behavior of clinically rabid animals might be a tenuous link in the circulation of the rabies virus. Some clinically rabid animals never have rabies virus in their saliva (Sikes 1962: 1045, Parker and Sikes 1966:943, Parker and Wilsnack 1966: 36). Some rabid animals may never develop the aggressive behavior associated with vicious biting attacks (Gough and Niemeyer 1975:176). There may also be a low probability that a clinically rabid animal could inflict a bite wound with the proper severity to insure an infection leading to clinical disease and, at the same time, a wound which is minor enough to avoid death or severe bacterial infection in the susceptible animal. An attack by a clinically rabid animal could result in many severe bite wounds which might cause death from a major bacterial infection before clinical rabies could occur. It is also possible that the clinically rabid animal might not be able to overtake and bite healthy animals in the field.

A carrion feeding mode of rabies transmission could be a more consistently effective means of rabies transmission. Susceptible animals with some carrion feeding behavior would be drawn to the carcass of a rabies infected animal, especially during times of reduced food supply. Several scavengers might feed on the same carcass. In such a transmission scheme the susceptible animals would actually facilitate their infection, and the rabies infected animal which may not have been a successful rabies vector in life would become a rabies vector after death. In fact, the predominance given to the bite transmission of rabies may represent an anthropocentric point of view. Human rabies is considered to be a major aberration in the natural circulation of the rabies virus, and the form of rabies transmission to man may not represent the dominant means of viral circulation among wild animals. Some people and domestic animals approach a rabid animal prior to being bitten, an action which many wild animals might readily avoid. After the death of the rabies infected animal, the degree of attraction might be reversed since the carcass would represent a food source to the scavenger and the ruination of a pleasant day to man.

In summary, it would appear that clinical rabies cases occur in animal populations which are either above the carrying capacity of the environment or declining in the face of environmental stress. In both situations the factors of stress, increased mortality, and behavioral changes in such areas as feeding habits could create an increase in clinical rabies cases and rabies virus transmission. Therefore, the ultimate method for controlling enzootic rabies and preventing large epizootics would be to insure population stability among predator/scavenger animals at levels which are in balance with the resources of the environment. Some evidence seems to point to human disruption of the environment as a factor in the emergence of clinical rabies cases in wildlife populations. The problem of clinical rabies in such alien animals as the mongoose (*Herpestes auropunctatus*) in the Caribbean and cattle rabies in South America may have resulted from man-made alterations and introduction into well balanced ecosystems. Similarly, the emergence of fox rabies problems in eastern Europe immediately after World War II certainly occurred in an environment ravished by man. The emergence of raccoon rabies in Florida may be related to the rapid development of that state for human needs. As in so many cases where man has cursed the malice of nature, the terrible scourge of clinical rabies may reflect the handiwork of man himself.

VITA

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